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The Relation of Weather to Population Trends of the Black-headed Budworm *Acleris variana* (Fern.) (Lepidoptera: Tortricidae)[1]

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Introduction

The history of the black-headed budworm, *Acleris variana* (Fern.), in the western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) forests of coastal British Columbia is one of recurring cycles of outbreaks. The latest cycle occurred from 1952 to 1957 and was represented by three main outbreaks in the Portland Canal area from Prince Rupert to Stewart, the Queen Charlotte Islands, and on northern Vancouver Island. Previous to this, groups of West Coast outbreaks were recorded from 1940 to 1945, and from 1927 to 1931 (Prebble and Graham, 1945a).

Biological studies on the outbreaks have to date been confined to the effects of parasites and virus disease on the populations, with some observations on the influence of weather on survival and development. During the recent outbreaks, observations and field records indicated that decreases in larval populations were associated with certain types of weather, particularly with respect to precipitation. Further examination indicated that the rise of the outbreaks was also related to precipitation. If it can be established that such trends are consistent, the Forest Insect Survey could develop a method for the prediction of the rise and decline of black-headed budworm populations which would be of invaluable assistance in planning and organizing annual surveys, and anticipating the need for control operations. This paper examines the association between certain weather patterns and fluctuating populations of black-headed budworm.

The life history of the black-headed budworm on northern Vancouver Island is as follows: Moth emergence starts about mid-August and is completed about mid-September. Adults are present in the field as late as the first week of October. The orange-coloured eggs are laid singly on the under sides of the needles of both new and old foliage. The winter is passed in the egg stage. Egg hatch begins about mid-May and is usually completed the first week of June. In 1956, eggs began to hatch when the buds started to open. The young larvae move into the opening buds and make a protected feeding site by webbing the needles together with silk. Feeding takes place in such protected sites for the first two instars and part of the third. The larvae then become free feeding for the remaining two instars. The larvae begin to pupate about mid-July, and pupation continues for about seven weeks.

There is considerable overlapping in stages present in the field at any one time.

Methods and Material

The population trends of the three recent outbreaks were obtained from Forest Insect Survey records. Northern Vancouver Island, because of its important hemlock stands and the heavy defoliation which eventually led to chemical control measures, received more attention than the two earlier infestations. The annual status of the outbreak was determined by larval samples, defoliation aerial surveys, and egg counts (Silver, 1959). The sampling method

[1]Contribution No. 611, Forest Biology Division, Research Branch, Department of Agriculture, Ottawa, Canada.

TABLE I

Development of black-headed budworm, northern Vancouver Island.

Larval stage	Peak of stage	
	1956	1957
I	May 15	May 29
II	June 1	June 4
III	June 19	June 15
IV	July 5	July 12
V	July 27	July 26
Pupal	Aug. 10	—

used in developmental studies in 1956 has been described (Brown *et al.*, 1958). Work was carried out at Port McNeill, Quatse Lake, and near Port Hardy in 1956, but only near Port Hardy in 1957. Records on the Queen Charlotte Islands and the Prince Rupert mainland were obtained chiefly from routine 3-tree beating collections, which consist of the number of larvae beaten off the branches of three trees onto a 7 x 9 foot sheet, a small number of egg counts, and a limited number of field observations.

Weather data were obtained from official weather stations in the outbreak areas. Analysis was first made at 10-day intervals, but to avoid long tables the data were grouped into longer periods of time.

For ease of description each infestation is considered separately.

Results

Northern Vancouver Island. The black-headed budworm increased in numbers in 1952 although the resulting population was still light. The increase continued in 1953, and the following year noticeable defoliation occurred, particularly around Holberg Inlet. By 1955 the infestation had assumed major proportions, covering an area of more than 1,600 square miles. In 1956 damage to trees occurred on some 3,000 square miles of which one-third was classified as heavily defoliated. In October, 1956, the number of eggs in the field decreased an average of 63 per cent compared with 1955. A general decrease in the number of larvae was observed in July, 1957, and by mid-August only a few were found in samples. The collapse of the outbreak was verified in October when the number of eggs decreased an average of 97 per cent compared with 1956. Only a few larvae were collected in the outbreak area in 1958.

For the development studies only 1956-57 records from the Port Hardy area were considered. The dates at which different larval instars were at their peak are shown in Table I. No pupae were found in 1957, but it was assumed that pupation occurred on about the same dates as in 1956.

The rate of development in relation to precipitation and temperature is shown in Table II. The time interval is the number of days from the peak of one stage to the peak of the next stage. Larval activity in 1957 started about two weeks later than in 1956, but the first instar was completed in a relatively short time. In 1956 the time for development from instar II to III was a week longer than in 1957, but rain fell for 16 of the 18 days. Temperatures were about the same, so the longer development time was definitely related to the prolonged rainy period.

TABLE II

Development of black-headed budworm larvae in relation to precipitation and temperature. Northern Vancouver Island.

	Instar development					
	Year	I-II	II-III	III-IV	IV-V	V-P
No. days	1956	11	18	16	22	14
	1957	6	11	27	14	16*
No. days with precipitation	1956	3	16	9	2	3
	1957	2	4	23	5	11
Inches rain	1956	0.23	2.47	1.07	0.45	0.24
	1957	0.07	1.39	6.19	1.66	2.79
Mean Max. Temp.	1956	62.6	58.1	57.8	65.5	63.7
	1957	65.7	59.5	59.5	61.6	61.5
Highest Temp.	1956	78	66	62	75	69
	1957	77	67	67	66	67

*As no pupae were found in 1957 the 1956 date was used (Table I).

In the next larval instar, 27 days were required in 1957 compared with only 16 the previous year. Here again rainy weather prevailed for 23 of the 27 days compared with only nine days of rain for the 16 days in 1956. Also, the amount of rain which fell during this period in 1957 was almost six times as much as in the year before. The amount of precipitation between instars IV and V was not excessive in either year, but development was considerably prolonged in 1956. The reason for this was probably a hot dry spell during which temperatures reached 75° F, which is quite rare for this area. The number of larvae per sample decreased on July 27 (Table III) but the population was not permanently

TABLE III

Number of black-headed budworm larvae collected at Quatse Lake check plot. Each sample consisted of ten 18-inch branch tips. 1956.

Date	No. larvae			Percentage dead larvae
	Living	Dead	Total	
June 1	138	0	138	0
June 19	150	18	168	10.7
June 23	124	12	136	8.8
June 27	141	19	160	11.9
July 1	107	14	121	11.6
July 5	82	18	100	18.0
July 12	43	15	58	25.9
July 27	12	1	13	7.7
Aug. 10	60*	32	92	34.8

*Including pupae.

TABLE IV

Number of black-headed budworm larvae collected at check plot B, northern Vancouver Island. Each sample consisted of twenty 18-inch branch tips. 1957.

Date	No. larvae			Percentage dead larvae
	Living	Dead	Total	
May 28	108	15	123	12.2
May 31	216	20	236	8.5
June 3	85	11	96	11.5
June 6	63	18	81	22.2
June 10	84	11	95	11.6
June 14	45	18	63	28.6
June 19	62	23	85	27.1
June 24	39	19	58	32.8
July 12	44	20	64	31.3
July 19	17	6	23	26.1
Aug. 1	6	17	23	73.9
Aug. 8	1	6	7	85.7

lowered as is shown by the large collection of August 10. It is believed that the larvae retreated into the tree crowns in an effort to find cooler locations, resulting in the reduced sample of July 27, and accounting for the large collection on August 10 by which time they had returned to the branch tips and in many cases had completed feeding and pupated. Development would also be retarded during such a hot spell as feeding was curtailed. Such reactions as described and assumed for this insect were noted in the more intensive study by Wellington (1948) of reactions of sixth-instar spruce budworm larvae to intense radiant heating.

Moth emergence in 1956 started on August 11, and was well underway by the fourth week in August. The first egg was found in the field on August 26, but although moths were numerous in all areas, sampling failed to reveal any appreciable number of eggs. On August 24 the weather turned cold and damp with little sun, and the maximum temperature ranged between 56° and 65° F. up to September 4. During this period the moths were mostly inactive, although a few pairs were observed mating. By the second week in September, eggs were found evenly distributed throughout the area, but not in the numbers anticipated. As the pupal population was considered healthy, the 63 per cent decrease in the number of eggs laid could be attributed to unsuitable weather conditions during a large portion of this mating and oviposition period.

In 1957 the number of black-headed budworm larvae per sample showed a definite decrease after mid-July and heavy larval mortality was evident by August 1 (Tables IV and V). By mid-August no larvae or pupae were found. The collapse of the outbreak was confirmed in October by an average 97 per cent decrease in the number of eggs compared with 1956. The last half of June and the first half of July were exceedingly wet in 1957. In the 30-day period from June 14 to July 13, 6.43 inches of rain fell in 24 days. This was considerably more precipitation than was recorded from May 5 to August 12 the previous year (Table VI). Field observations indicate that feeding by the black-headed budworm is severely curtailed during rainy periods. In this example the heavy larval mortality occurred after the unfavourable weather was over. No experiments were conducted to study the effect of prolonged rainy periods on larval activity, but the larvae were apparently weakened.

TABLE V

Number of black-headed budworm larvae collected at check plot 11. Northern Vancouver Island. Each sample consisted of twenty 18-inch branch tips. 1957.

Date	No larvae			Percentage dead larvae
	Living	Dead	Total	
May 29	142	23	165	13.9
June 3	71	6	77	7.8
June 18	49	22	71	31.0
June 21	60	13	73	17.8
June 24	38	9	47	19.1
July 10	42	37	79	46.8
July 17	15	25	40	62.5
Aug. 1	2	12	14	85.7
Aug. 8	1	10	11	90.9

The same general weather conditions as in 1957 existed in 1956 when the larvae were in the third instar, but mortality was not heavy. The feeding habits of the black-headed budworm afford one explanation. The first two instars and most of the third are spent in the flushed buds where the larvae are relatively well protected by silk webbing. Although development would be slowed, the rain would not have the same adverse effect as it would on the older, free-feeding larvae. This was also pointed out by Prebble and Graham (1948b) who stated . . . . "large numbers of young larvae have become successfully established in years characterized by heavy rainfall in May and June, and the role of weather at this stage of budworm development certainly has not been of much direct importance in the current outbreak."

As records on development are not available before 1956 no earlier direct comparisons are possible. Precipitation records for the years 1950 to 1957 are shown in Table VI. The records are divided into three time periods, the period June 14 to July 13 being considered the critical period as the larvae were then

TABLE VI

Summary of precipitation records at Port Hardy Airport.

	Time period				
	Year	May 5-June 13	June 14-July 13	July 14-Aug. 12	Total
Total days with rain	1950	22	14	10	46
	1951	17	6	10	33
	1952	18	14	4	36
	1953	18	15	12	45
	1954	17	21	9	47
	1955	20	13	13	46
	1956	19	14	4	37
	1957	14	24	17	55
Inches of rain	1950	4.00	2.52	1.80	8.32
	1951	4.77	0.99	1.14	6.90
	1952	2.15	2.94	0.54	5.63
	1953	2.07	2.24	2.12	6.43
	1954	1.70	2.91	1.71	6.32
	1955	4.27	2.95	2.11	9.33
	1956	1.91	2.18	0.65	4.74
	1957	2.57	6.43	4.37	13.37

TABLE VII

Precipitation records from the Prince Rupert weather station.

Year	No. days with rain		Inches precipitation	
	June 20-July 19	July 20-Aug. 18	June 20-July 19	July 20-Aug. 18
1950	21	18	3.91	6.30
1951	10	18	1.52	4.38
1952	13	13	3.02	1.06
1953	18	14	3.47	2.88
1954	19	23	4.17	4.15
1955	13	22	3.00	10.91

entering or in the free feeding stage. The black-headed budworm increased in numbers following the drought years of 1951 and 1952, and continued to increase until it reached its height in 1956. During this time precipitation in the June 14-July 13 period did not exceed three inches until 1957 when 6.43 inches of rain fell in 24 days. In 1954 rain was recorded on 21 days, but the total rainfall was only 2.91 inches. The total days with rain, and the total amount of precipitation for the eight year period was greatest in 1957, both for the 30-day period and for the entire summer.

Precipitation records from Quatsino and Port Alice were very similar to those from Port Hardy. The rainy periods were also similar to Port Hardy in respect to the distribution of the times at which they occurred. The general weather pattern was therefore similar throughout the heavy infestation area.

Prince Rupert-Stewart. Black-headed budworm larvae were common in the Prince Rupert-Stewart area in 1949, but the population remained at a low level until 1952 when a definite increase became noticeable. The outbreak reached its height in 1953, resulting in defoliation of western hemlock from Prince Rupert north along the Portland Canal to the head of Alice and Hasting arms. In that year parasites killed 34 per cent of the larvae in this region.

In 1954 the budworm population developed normally until mid-July. Fifteen points sampled in the Prince Rupert area in mid-July averaged 84.7 larvae per 3-tree beating sample; the same points averaged only 17.8 larvae when resampled in early August, a decrease of 79 per cent. Development was greatly retarded. In early August the larvae were small and the bodies were yellowish in colour rather than the characteristic green. A large number of dead and dying larvae were examined by an insect pathologist but no evidence of virus disease was found. Defoliation was very light with no obvious feeding from mid-July onward. Very few larvae were collected in 1955, and none in 1956.

Precipitation records from the Prince Rupert weather station are shown in Table VII. As there were no data on development, the records on precipitation were arbitrarily divided into two groups, June 20 to July 19, and July 20 to August 18. These two time periods include the greater, and what is considered, the most critical portion of the feeding period.

At Prince Rupert, 1950 was a relatively wet rainy year, and as indicated by survey records the budworm population remained at a low level. The next year

TABLE VIII

Precipitation records from Sandspit Airport weather station.

Year	No. days with rain		Inches precipitation	
	June 20-July 19	July 20-Aug. 18	June 20-July 19	July 20-Aug. 18
1950	18	16	3.50	1.92
1951	7	13	0.54	1.68
1952	8	3	0.73	0.25
1953	10	11	1.56	2.47
1954	19	11	2.25	1.67
1955	13	16	1.06	2.37
1956	11	10	1.24	0.80
1957	21	12	5.15	2.81
1958	2	12	0.04	2.04

had fewer rainy days and an over-all decrease in rainfall. As a population increase was observed in 1952, conditions must have been sufficiently good to allow such an increase. From the standpoint of precipitation, 1952 was the driest year with the lowest number of days and the smallest amount of rain. The results of this dry year were reflected in the attainment of the height of the larval population in 1953. Between July 20 and August 18, 1954, rain fell at Prince Rupert for 23 out of 30 days, and the number of days with rain for the entire summer was greater than in any of the four previous years. The first marked decrease in larval populations occurred during this prolonged wet period. Finally the amount of rain which fell during the same period in 1955 was the heaviest in six years. Survey information indicated that the budworm population was very light that year.

Weather records at Stewart show that a similar trend occurred in the upper portion of the outbreak. The area received less rainfall on an average than the coastal Prince Rupert region, an exception being 1952. However, there were only three days with rain in the July 20-August 18 period, thus presenting the black-headed budworm with good weather for about four weeks. The long rainy period experienced at Prince Rupert in 1954 did not occur at Stewart, but 1955, the year in which the outbreak collapsed in this area, was once again the wettest of the six years considered.

Queen Charlotte Islands. Black-headed budworm larvae averaged 0.1 larvae per sample in 1949, and 1.0 in 1950, but a definite upward trend was not noted until 1952 when collections in the Queen Charlotte Islands averaged 26.2 larvae each. The population increased more than 4-fold in 1953, and reached its peak in 1954. The heaviest populations were found near Masset, and from Alliford Bay to Skidegate Lake. Larvae decreased from an average of 225 per sample in 1954 to 89 in 1955. No eggs were found in September or October, 1955, and the collapse of the outbreak was confirmed when no larvae were found in 1956. There is little doubt that the outbreak collapsed in the late larval period of 1955. No pupae were found and no moths observed during the egg survey.

Parasitism was very light from 1952 to 1954, and in 1955 parasites killed only 30 per cent of the larvae.

Weather records from Sandspit Airport (Table VIII) and Masset were analysed. Those for Masset are not given as they are similar to Sandspit. Weather conditions improved in 1951 compared with the previous year, and this improvement was reflected in the substantial increase in larvae in 1952 which was

a drought year. Significantly, the budworm population had increased four-fold by 1953. The outbreak reached its height in 1954, despite 1953 being wetter than the previous two years. The number of days with rain increased in 1954 compared with the previous year, and although the larval counts were highest that summer the relative number of eggs in the fall of 1954 had decreased by about 57 per cent compared with 1953. In 1955 precipitation during the June 20-July 19 period was below the average or equal to the previous two years, but the number of days with rain and the inches of rainfall were greater in the July 20-August 18 period than the previous year and at Masset the heaviest in six years. Egg counts were extremely low in 1955 (0.01 eggs per 18-inch branch sample compared with 11.3 in 1954 and 26.2 in 1953), and only three larvae were collected in 1956.

Although the relationship between rainfall and the rise and fall of the black-headed budworm was not as clear as in the other two outbreaks, the same trend was present. Since only very limited field observations were possible, there are no records on the condition of the population.

One further association of weather and the rise of black-headed budworm outbreaks is available. Following the collapse of the outbreak in 1955, the weather at Sandspit improved considerably in 1956. A small increase in the budworm population was observed by 1957, which was a particularly wet year, both at Sandspit and at Masset. In 1958, however, there was another drought in coastal British Columbia, and this was reflected in the records, particularly at Sandspit and to a lesser degree at Masset. Moths were observed in relatively large numbers on Moresby Island during a late survey of the Queen Charlotte Islands. By 1959, the black-headed budworm was present throughout Moresby Island in far greater numbers than in their previous peak year of 1954, and larvae were found in large numbers on Graham Island, although the number of larvae per sample decreased northward from Sandspit and were considerably lower around Masset where weather was less favourable.

Discussion

In studies of this kind, there is always a danger of attempting to isolate one weather factor and relate it to population fluctuations. It was expected that temperature records could not always be correlated with population trends. In an analysis of spruce budworm infestations it was impossible to obtain any consistent relation between air temperature, changes and population changes (Wellington *et al.*, 1950). Prolonged wet or dry periods produce changes in other factors such as relative humidity, hours of sunshine, and temperature itself, so that a study based on precipitation also involves these other factors indirectly. As with the spruce budworm there it little doubt that the black-headed budworm has specific reactions and requirements. Precipitation was, however, the only weather factor which could be related directly to the population trend of the black-headed budworm.

Observations and periodic records on the development of the black-headed budworm indicate that weather plays an important role in the rate of development during the larval stages (Table II). It was shown that excessive precipitation in the earlier larval periods did not affect the over-all population trend, but it did tend to extend the length of time the budworm was in any particular instar. A prolonged hot period also had a similar effect on the older larvae, reducing feeding and retarding their rate of development. The decrease in the number of eggs on northern Vancouver Island in 1956 was associated with wet, damp, and below average temperatures during a considerable portion of the mating and oviposition period of the adults.

The increases in black-headed budworm populations were observed to follow one or two relatively dry years. More specifically, lower than average rainfall during the months of July and August preceded the increases in budworm population. Small increases in the budworm population were detected in some areas prior to the drought years, but the large increases followed the drought years of 1951 and 1952, and in the latest example, 1958. It is now established from Forest Insect Survey records that, although the black-headed budworm population drops to extremely low levels following the collapse of outbreaks, a few larvae and eggs can usually be found in routine sampling. After an outbreak subsides there is a low, more or less evenly distributed population throughout the coastal hemlock stands. This was the case on the Queen Charlotte Islands, and the same trend was apparent on northern Vancouver Island, where larvae were collected in more areas in 1959 than in 1958, although the number of larvae per sample was small.

The three black-headed budworm infestations followed a similar and characteristic pattern by remaining at a high level for only one or two years. On northern Vancouver Island and the Queen Charlotte Islands there was a decrease in the number of eggs laid the year before the final collapse, but in all cases the final collapse occurred during the late larval stage, and was associated with above average precipitation which occurred then. In some instances the absolute amount of rainfall was not excessive, but precipitation records are rough indices of both moisture and available sunlight, and the factors of excess moisture and lack of sunlight are probably unfavourable for the survival of larvae as indicated by the highest larval mortality coinciding with an increase in the number of rainy days.

Very little has been mentioned concerning the role of parasites and virus disease. There was no record or indication of a disease in the field populations. Parasites were present in varying numbers. The percentages of larval mortality attributed to parasitism on the Queen Charlotte Islands and the Prince Rupert mainland were not heavy enough to give any effective control. On northern Vancouver Island the maximum larval mortality from parasitism was 60 per cent, but the average was much lower. The average rate of parasitism was not considered sufficient to affect the population trend seriously.

Summary

The budworm populations increase greatly immediately following one or two years of below average precipitation during July and August. Further substantiation of this relationship is found in the 1959 outbreak in the Queen Charlotte Islands which appeared directly after the drought year of 1958. Populations reach their peak in two or three years. The three outbreaks studied all decreased and collapsed during or immediately following periods of heavier than usual precipitation during the latter portion of the larval development stages. Although weather effects on the black-headed budworm have not been explored experimentally, the repetition of the same general pattern of events in nature strongly suggests that annual weather conditions could be very useful in predicting black-headed budworm outbreaks even with our present information.

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The Immature Stages of Scolytidae: The Tribe Xyloterini[1]

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Introduction

Larval anatomy as an aid to understanding taxonomic and phylogenetic relationships of Scolytidae has been discussed in an earlier paper (Thomas, 1957). Before an appreciation of relationships can be gained, however, comparative descriptions of many species must be compiled. As representative groups of species become available, the immature stages of genera will be described, defining characters of value in separating component entities.

The tribe Xyloterini consists of the genera *Trypodendron* Stephens, *Xyloterinus* Swaine, and *Dendrotrypum* Schedl. According to a recent paper by Wood (1957), *Trypodendron* has about a dozen species, *Xyloterinus* is monospecific, and *Dendrotrypum* consists of six species known only from eastern Asia. The larvae and pupae of four of the five North American species of *Trypodendron*, *T. lineatum* (Olivier), *T. retusum* (Leconte), *T. rufitarsis* (Kirby), and *T. betulae* Swaine, of *Xyloterinus politus* (Say), and the larvae only of *Dendrotrypum aceris* (Niisima) were studied.

The specimens of *Trypodendron* were collected for the most part in the vicinity of Black Sturgeon Lake, southwest of Lake Nipigon, Ontario, and from Vancouver Island, British Columbia. Specimens of *X. politus* were collected at Fredericton, New Brunswick, and the larvae of *D. aceris* came from Hokkaido Island, Japan.

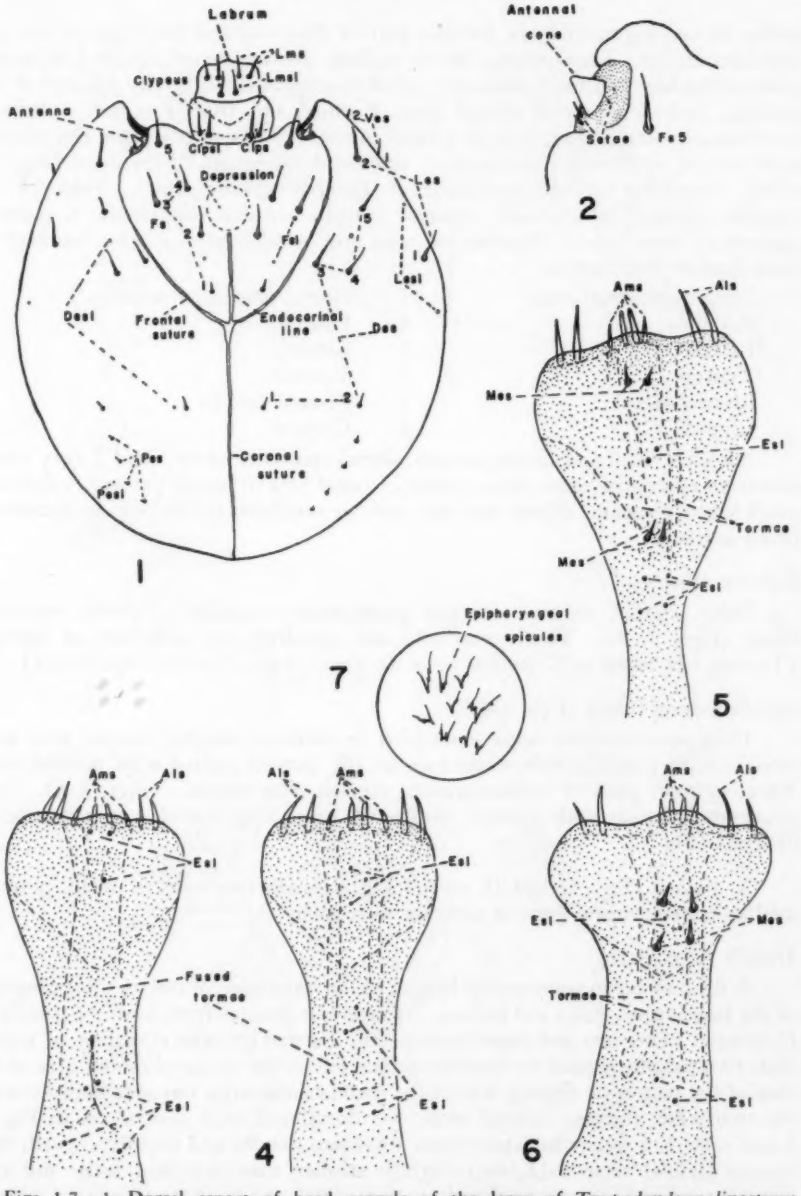
Description

The details of the following description apply directly to the genus *Trypodendron* and any differences in the anatomy of either of the other two genera are noted. The terminology used is that described in detail by Thomas (1957).

Head (Fig. 1)

Slightly longer than wide, widest at or near the middle, sides curved, posterior margin broadly rounded; partially retracted into the prothorax; mostly light

[1]Contribution No. 618, Forest Biology Division, Research Branch, Department of Agriculture, Ottawa, Canada.



Figs. 1-7. 1, Dorsal aspect of head capsule of the larva of *Trypodendron lineatum;* 2, Antenna of larva of *T. lineatum;* 3 and 4, Ventral aspect of epipharyngeal lining of the larva of *T. lineatum;* 5, Ventral aspect of epipharyngeal lining of the larva of *X. politus;* 6, Ventral aspect of epipharyngeal lining of the larva of *D. aceris;* 7, Enlargement of the integumental spicules on the epipharyngeal lining at the entrance to the pharynx. Als, Anterolateral setae; Ams, Anteromedian setae; Clps, Clypeal setae; Clpsl, Clypeal sensilla; Des, Dorsal epicranial setae; Desl, Dorsal epicranial sensilla; Esl, Epipharyngeal sensilla; Fs, Frontal setae; Fsl, Frontal sensilla; Les, Lateral epicranial setae; Lesl, Lateral epicranial sensilla; Lms, Labral setae; Lmsl, Labral sensilla; Mes, Median epipharyngeal setae; Pes, Posterior epicranial setae; Pesl, Posterior epicranial sensilla; Ves, Ventral epicranial setae.

amber to non-pigmented, the anterior part of the frons and the edges of the oral foramen darker. Frons triangular in outline, posterior end rounded to acute, endocarinal line indistinct anteriorly; shallow depression centrally located at the anterior limit of the endocarinal line. Coronal and frontal sutures indistinct. Antenna a conical segment set in a basal membranous area bearing a few minute setae two of which are approximately one-third the length of the cone (Fig. 2). (Only one long seta in specimens of *Dendrotrypum aceris*). Sides of the clypeus angulate to rounded, anterior margin broadly emarginate, a narrow, pigmented basal band. Number of setae and sensilla listed are for one-half of head capsule and clypeus.

Dorsal epicranial setae	5	Dorsal epicranial sensilla	3
Posterior " "	4	Posterior " "	1
Lateral " "	2	Lateral " "	2
Ventral " "	2	Ventral " "	1
Frontal setae	5	Frontal sensilla	2
Clypeal "	2	Clypeal "	1

All setae small and inconspicuous; dorsal epicranial setae 1 and 2 very short, posterior epicranial setae very minute, frontal seta 1 usually absent, extremely small when present. (Only one seta and no sensillum on clypeus in specimens of *D. aceris*.)

Labrum (Fig. 1)

Sides parallel, anterior margin protuberant medially. Tormae variously fused (Figs. 3, 4). Three setae and one sensillum on each side of labrum. (Tormae not fused in *X. politus* or in *D. aceris*, Figs. 5 and 6 respectively).

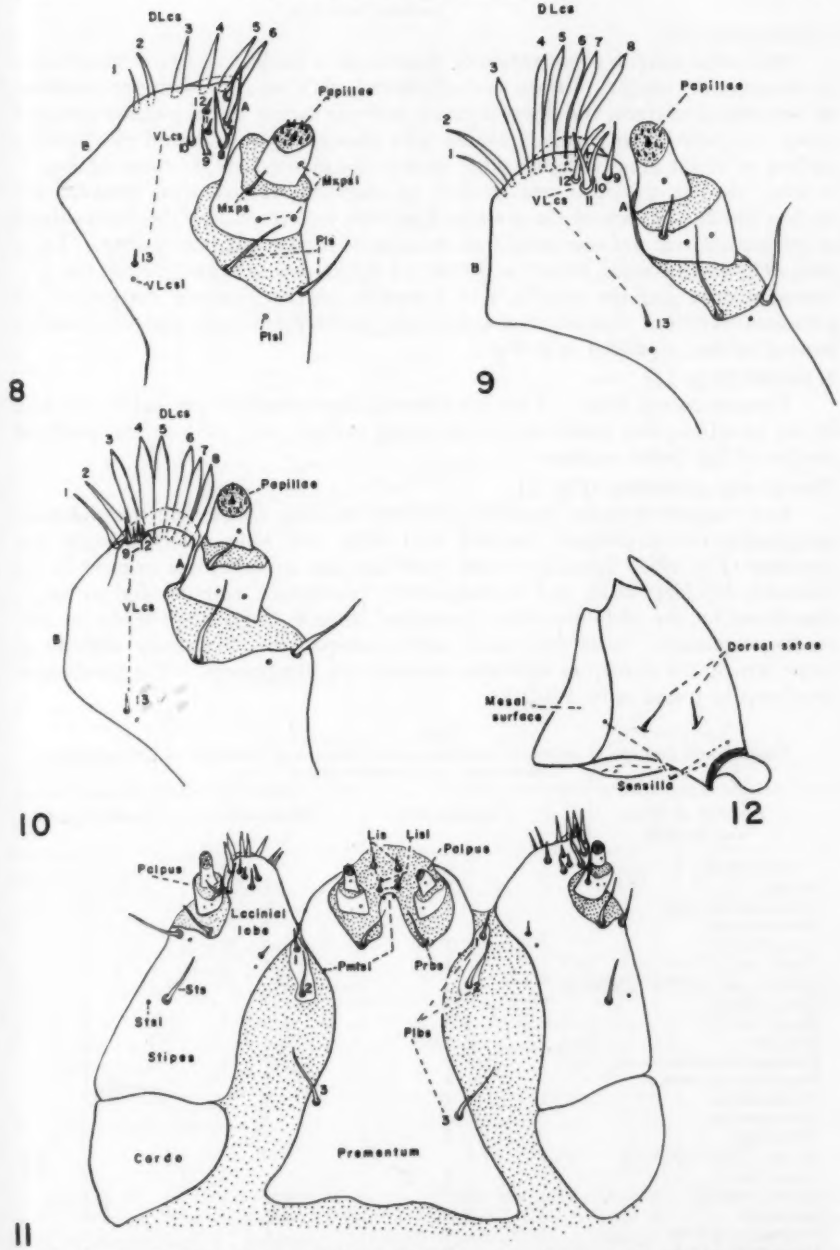
Epipharyngeal lining (Figs. 3-6)

Four anteromedian setae embedded in anterior margin; central two setae straight with rounded ends, outer two usually curved inward with pointed ends. Three or more pairs of median sensilla, median setae absent. (Figs. 3, 4). Epipharyngeal lining with minute backward projecting spicules at entrance to pharynx (Fig. 7).

X. politus (Fig. 5) and *D. aceris* (Fig. 6) with two pairs of small, pointed, median epipharyngeal setae in addition to sensilla.

Maxilla (Figs. 8-11)

A distinct cardo transversely hinged to the remainder of the maxilla composed of the fused stipes, galea and lacinia. (Cardo not distinct from body of maxilla in *D. aceris*). One seta and sensillum centrally located on ventral surface of stipital area; two palpiferal setae on ventral surface on border of membranous area at the base of the palpus or slightly within the membranous area, one sensillum between the two setae; thirteen lacinial setae, 1-5 dorsal and 6-13 ventral, as in Fig. 8; dorsal setae 1, 2 somewhat apart from 3-6, more slender and slightly curved; four ventral lacinial setae 9-12, two slightly smaller than marginal setae and two minute, arranged in a group slightly mesad of 6, 7 and 8. Seta 13 minute with an adjacent sensillum. (Setae 1-8 distally located on dorsal surface in *D. aceris* and *X. politus* Figs. 9, 10) (Ventral lacinial setae 9-12 on small raised lobe in *D. aceris*, Fig. 10). Palpus two-segmented, the basal segment widest bearing on its ventral surface a short seta and two sensilla; the distal segment with one sensillum on ventral surface and from six to twelve small papillae grouped about a slightly larger central papilla on the apex of the segment.



Figs. 8-12. 8, Ventral aspect of the lacinial lobe and palpus of the maxilla of the larva of *T. lineatum;* 9, Ventral aspect of the lacinial lobe and palpus of the maxilla of the larva of *X. politus;* 10, Ventral aspect of the lacinial lobe and palpus of the maxilla of the larva of *D. aceris;* 11, Ventral aspect of the labium and maxillae of the larva of *T. lineatum;* 12, Dorsal aspect of the mandible of the larva of *T. lineatum.* Dlcs, Dorsal lacinial setae; Lis, Ligular setae; Lisl, Ligular sensilla; Mxps, Seta on maxillary palpus; Mspsl, Sensilla on maxillary palpus; Plbs, Postlabial setae; Pls, Palpiferal setae; Plsl, Palpiferal sensilla; Pmtsl, Premental sensilla; Prbs, Prelabial setae; Sts, Stipital setae; Stsl, Stipital sensilla; VLcs, Ventral lacinial setae; Vlcsl, Ventral lacinial sensilla.

Labium (Fig. 11)

Premental sclerite subquadrate in shape with a median and two lateral arms on the anterior margin. Palpus two-segmented, each segment with one sensillum on the ventral surface, the distal segment with six to ten apical papillae grouped about a slightly larger papilla. Ligula with four to eight setae and two sensilla; surface of distal area of ligula with minute spicules similar to those in Fig. 7. A long, slender, prelabial seta in each of the membranous areas between the median and lateral arms of the premental sclerite; two sensilla on the distal margin of the median arm and one sensilla on the base of each of the lateral arms. Three pairs of postlabial setae, setae 1 and 2 on a long narrow sclerite between the premental sclerite and the maxilla, seta 3 usually on the posterior margin of the premental sclerite. Postlabial area between premental sclerite and the maxillae bearing minute asperities as in Fig. 7.

Mandible (Fig. 12)

Three incisoral teeth. Two setae on the dorsal surface parallel to the base of the mandible; one sensillum on the mesal surface, and two on the proximal margin of the dorsal surface.

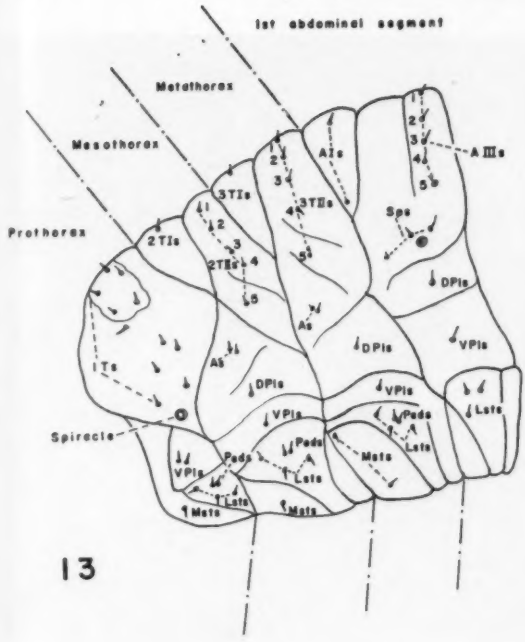
Thorax and Abdomen (Fig. 13)

Body convex dorsally, apodous, prothorax slightly wider than the abdomen. Integument non-sclerotized, marked into folds and lobes, clothed with fine asperities (Fig. 14). Spiracles on the prothorax and segments one to eight of the abdomen, circular, small, and inconspicuous; prothoracic spiracle slightly larger than those on the abdomen; first abdominal spiracle larger than those on succeeding segments. Setae very small and inconspicuous, frequently difficult to locate among the numerous asperities covering the integument. The numbers of setae usually found as in Table I.

TABLE I

Number and position of setae and sensilla on the thorax and abdomen of *Trypodendron*, *Xyloterinus*, and *Dendrotrypum*.

Position of Setae and Sensilla	*Trypodendron*	*Xyloterinus*	*Dendrotrypum*
PROTHORAX			
Dorsal	11	11	11
Ventropleural lobe	2	2	2
Mediosternal	1	1	1
Laterosternal	3	3	3
Pedal lobe	2	2	2
MESO- and METATHORAX			
Dorsal fold I	1	1–2	1
Dorsal fold II	4–5	4–5	4–5
Alar area	2–4	2–4	2
Dorsopleural lobe	1	1	1
Ventropleural lobe	1	1	1
Mediosternal	2	2	2
Laterosternal	3	3	3
Pedal lobe	2	2	2
1st.-8th. ABDOMINAL			
Dorsal fold I	2	2	2
Dorsal fold III	4–5	4–5	4–5
Spiracular	2–3	2–3	2–3
Dorsopleural lobe	1	1	1
Ventropleural lobe	1	1	1
Mediosternal	0	0	0
Laterosternal	3	3	3
9th ABDOMINAL			
Dorsal	3	3	3
Pleural	2	2	2
Sternal	2	2	2



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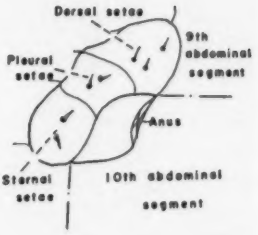

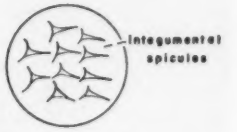

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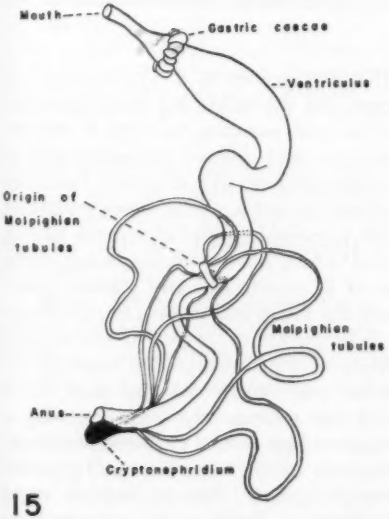

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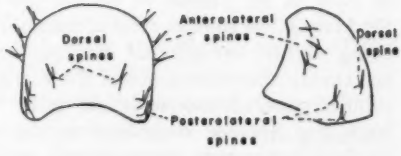

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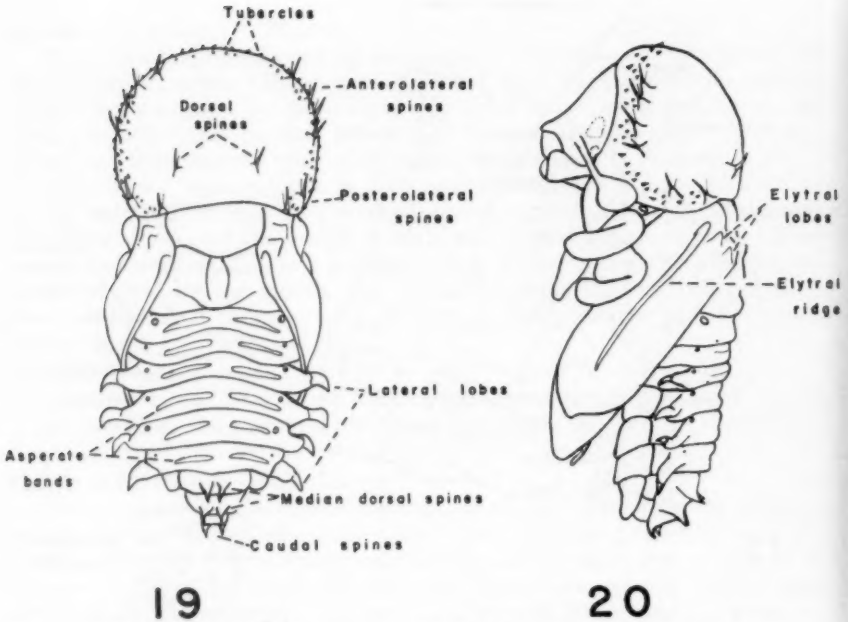
Figs. 13-18. 13, Lateral aspect of thorax, 1st, 9th, and 10th abdominal segments of larva of *T. lineatum;* 14, Enlargement of the integumental spicules of the larva; 15, Alimentary canal of the larva of *T. lineatum;* 16, Dorsal aspect of the pronotum of the pupa of *T. lineatum*, male; 17, Dorsal aspect of the pronotum of the pupa of *X. politus*; 18, Lateral aspect of the pronotum of the pupa of *X. politus*. AIs, Setae on fold I of abdomen; AIIIs, Setae on fold III of abdomen; As, Alar setae; DPIs, Dorsopleural lobe setae; Lsts, Laterosternal setae; Msts, Mediosternal setae, Peds, Setae on pedal lobe; Sps, Spiracular setae; VPIs, Ventropleural lobe setae; 1Ts, Setae on prothoracic dorsum; 2TIs, Setae on fold I of mesothorax; 2TIIs, Setae on fold II of mesothorax; 3TIs, Setae on fold I of metathorax; 3TIIs, Setae on fold II of metathorax.



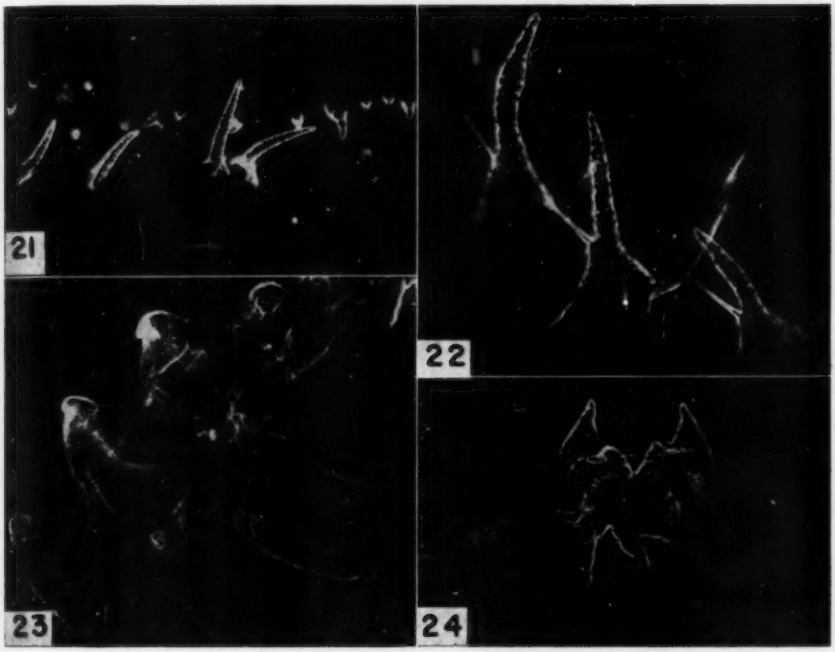
Figs. 19, 20. *T. lineatum*, pupa. 19, dorsal aspect; 20, lateral aspect.

Alimentary Canal (Fig. 15)

The alimentary canal of the larvae of the four species of *Trypodendron*, of *X. politus* and *D. aceris* was similar in structure and the following description for *T. lineatum* is applicable to all. The pharynx and oesophagus form a narrow tube through the head and thorax, there being no well-defined proventriculus as there is in the adults. The ventriculus is an expanded sac-like structure followed by a relatively narrow tube, the anterior intestine or ileum. The development of gastric caeca at the anterior of the ventriculus is variable, some specimens having all the caeca more or less uniform in size, and others having various sized caeca or none at all. None of the six specimens of *D. aceris* had any gastric caeca. Six Malpighian tubules arise at the point where the ileum and colon join, the ileum being slightly invaginated into the colon. The points of origin of the tubules are evenly distributed about the circumference of the intestine and four of the tubules proceed anteriorly alongside the ileum and ventriculus and then curve back and become embedded in the wall of the rectum, the ends forming a thickened structure alongside the anal opening. This is the cryptonephridium. Two of the tubules are about one half the diameter of the other four and proceed almost directly to the rectum and cryptonephridium. The alimentary canal shown in Fig. 15 has been stretched out in order to facilitate drawing and the orientation of the various parts is not correct. Normally the anterior and posterior intestines are compressed and looped about each other with the Malpighian tubules more entwined about them.

Pupa (Figs. 19, 20)

Head concealed from above. Pronotum wider than long, anterior margin and sides rounded in female (Fig. 19); anterior margin less rounded in male with



Figs. 21-24. 21. Photomicrograph of anterolateral spines and tubercles on the pronotum of the pupa of *T. lineatum*. 22. Photomicrograph of the anterolateral spines on the pronotum of the pupa of *X. politus*. 23. Photomicrograph of the asperate bands and lateral spines on the abdomen of the pupa of *T. lineatum*. 24. Photomicrograph of the asperate spines on segments 7, 8, and 9, of the abdomen of the pupa of *T. lineatum*.

median notch, sides sub-parallel (Fig. 16). Anterior and side margins with a ring of small asperate tubercles of varying size (Figs. 19, 20, 21). Four anterolateral, two posterolateral, and one dorsal spine on each half of pronotum; spines on a rounded basal protuberance bearing a long, slender seta; the base and spine both asperate (Fig. 21).

In *X. politus* anterior margin of pronotum rounded, sides sub-parallel; no ring of tubercles about the pronotum (Fig. 22); three anterolateral spines (Figs. 17, 18). (No pupae of *D. aceris* available for comparison).

Elytra with a longitudinal ridge and two basal protuberances (Fig. 20).

Nine abdominal segments visible dorsally, segments one to six with a pair of asperate transverse bands, segments three to six with paired asperate lobes projecting laterally (Figs. 19, 23). Segments seven and eight with a pair of asperate spines, medially located, projecting postero-dorsally, a pair of caudal spines on segment nine (Figs. 19, 24). A mesothoracic spiracle and spiracles on abdominal segments one to six, opening on segment six being rudimentary or absent.

Discussion

The tribe Xyloterini can be distinguished from other groups in the classification of Scolytidae, as understood at present, by a combination of adult characters outlined by Wood (1957). A single larval character has been found that also links the three genera of the tribe and at the same time sets them apart from all

other scolytids studied so far. In the general study of Scolytid beetles (Thomas, 1957), it was found that in *Trypodendron* the premental sclerite of the labium was subquadratic in shape with a median and two lateral projections from the anterior margin, as opposed to its trident shape in all others studied. This peculiar shape is also a characteristic of *Xyloterinus* and *Dendrotrypum*.

Although the larvae of all species in the tribe are markedly similar, they can be separated on a generic level by the shape of the lacinial lobe and by the position and shape of the dorsal and ventral lacinial setae. Outlines of the typical lacinial lobe in each genus are shown in Figs. 8, 9, 10, in which the margin nearest the maxillary palpus is designated "A" and the opposing margin nearest the labium is designated "B". In *Trypodendron*, "B" is at an angle of approximately 45° to "A" (Fig. 8), whereas the sides are more or less parallel in *X. politus* and *D. aceris* (Figs. 9 and 10). The anterior margin of the lobe in *D. aceris*, however, is more rounded than that in *X. politus*. Usually at least three of the large lacinial setae are ventrally located along margin "A" in *Trypodendron* with a second group of four ventral lacinial setae (9-12) mesad to these. All eight of the large lacinial setae are dorsally located along the anterior margin in *X. politus* and *D. aceris*. Ventral lacinial setae (9-12) are located on a small projecting lobe in *D. aceris* (Fig. 10). In all three genera, setae 1 and 2 are slightly separated from the remainder, are usually smaller and slightly curved, and taper evenly from the base to a sharp point. In *Trypodendron*, the remaining setae begin to taper near the base, but these setae have sub-parallel sides and taper to a point only at the extremity in *X. politus* and *D. aceris*.

Characters on the pronotum of the pupae separate *Trypodendron* and *Xyloterinus*. No pupae of *D. aceris* were available for comparison. Typically there are four anterolateral spines on pupae of *Trypodendron* (Figs. 19, 20, 21), but the number varied usually by plus or minus one on one or both sides. The variation affected 20 per cent of the *rufitarsis*, 21 per cent of the *retusum*, 24 per cent of the *lineatum*, and 28 per cent of the *betulae* pupae. In contrast, all specimens of *X. politus* invariably had three anterolateral spines on each side (Figs. 17, 18, 22). Although errors in generic determination are possible using the number of spines alone, a second character was found to be completely reliable. A band of tubercles of varying size, but always smaller than the spines described above, encircles the anterior and lateral margins in *Trypodendron* (Figs. 19, 20, 21), but is absent from *X. politus* (Fig. 22).

Although Wood (1957) found reliable characters for separating the adults of the five North American species of *Trypodendron*, a study of the external and internal anatomy of the four available failed to reveal diagnostic larval or pupal characters. A point of interest is the considerable range of intra- and interspecific variation in the number of ligular setae and sensilla, and the anteriorly situated, premental sensilla (Fig. 11). In three species, *lineatum*, *rufitarsis*, and *betulae*, 75 to 78 per cent of the specimens had four ligular setae; the remaining specimens had five or six. The increase of one or two setae over the typical number, four, was in most cases accompanied by a corresponding decrease in the number of ligular or premental sensilla, suggesting modification from one to another type of sensory organ. Occasionally a specimen had fewer sensilla than could be accounted for by increase in number of setae but only rarely were there more than eight setae, the number of setae and sensilla usually present. Only four of 38 specimens of *T. retusum* had four ligular setae, the remainder had from five to nine with the majority (26) having six. Again, most of the increases in the number of setae corresponded with decreases in the number of ligular and premental sensilla. Unfortunately, all the specimens of *T. retusum*

were from one locality and it cannot, therefore, be said at present whether this difference in ligular setae can be used to separate *retusum* from the remaining three species of *Trypodendron* or whether it merely represents a geographical variation.

Acknowledgments

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Biology of the Diamondback Moth, *Plutella maculipennis* (Curt.) (Lepidoptera: Plutellidae), in Eastern Ontario
III. Natural Enemies

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The diamondback moth, *Plutella maculipennis* (Curt.), is a sporadic pest of cruciferous crops throughout Canada. It is normally held in check by a multiplicity of environmental factors, chiefly biotic; however, serious outbreaks do occur (MacNay, 1948, 1953, 1957, 1959). In eastern Ontario it has been extremely numerous since late 1951, and during the present study, 1952 - 1956, it was more abundant than the imported cabbageworm, *Pieris rapae* (L.), or the cabbage looper, *Trichoplusia ni* (Hbn.). Two earlier papers (Harcourt, 1956, 1957) presented the history, distribution, and synonymy of the insect, giving general descriptions of the stages and many aspects of its biology in eastern Ontario. This article gives the relative abundance of its parasites and predators, and discusses certain population relationships.

General Methods

This investigation was carried out in long-term study plots at a 10-acre field station at Merivale, Ontario, five miles south of Ottawa. Although experiments were largely confined to this locality, observations were made throughout eastern Ontario during the five years of the study. Frequent spot checks indicated that parasite-host relationships at Merivale were representative of the larger area. At no time were insecticides used in or near the study plots.

Cabbage was the crop used in experiments because it is readily grown, and populations of the host on it are representative of those on other cultivated crucifers (Harcourt *et al.* 1955). Cultural methods were the same as practised commercially in the area. Crops of both early and late cabbage were grown each year in adjacent quarter-acre fields. The early crop, which matured in July, was planted in late May; the late crop, which matured in October, was planted in late June. These provided a succession of crops throughout the summer.

TABLE I

Parasitism of larvae of the diamondback moth by *M. plutellae* and *H. insularis*, Merivale, Ont., 1956

Instar	Number collected	Percentage parasitized	
		M. plutellae	*H. insularis*
I	146	0.0	15.8
II	302	1.3	31.1
III	353	2.5	52.4
IV	296	2.7	47.3
Total	1097	1.9	40.3

To obtain data on parasites that kill the host in the prepupal and pupal stages, cocoons of *P. maculipennis* were collected at weekly intervals. Generally, six collections of at least 100 cocoons were made from the early crop, and 12 from the late. The cocoons were collected at random, and reared in small gelatin capsules individually in the laboratory.

Data on parasites that kill the feeding larvae were obtained principally by rearing large samples of caterpillars taken periodically from each crop. Eggs were collected once every two weeks throughout the season, and reared until they hatched in the laboratory.

Most of the data on behaviour of the parasites and predators were obtained by observation in the field. *Horogenes insularis* (Cress.) was studied also in the laboratory.

Insect Parasites

Parasites of the Eggs

No egg parasites were observed during the investigation. No record of egg parasitism of the species in nature has appeared in the literature. Veitch (1929) described studies in Australia with *Trichogramma minutum* (Riley) in which the parasite attacked eggs of *P. maculipennis* in the laboratory but did not do so in the field.

Parasites of the Larvae

Horogenes insularis (Cress.).—This was the principal parasite of the diamondback moth at Merivale, attacking the larvae from early June until late October. Populations of the parasite were low each year during June and early July, but rose with populations of their host, reaching a peak at the beginning of September. In the field, *H. insularis* attacked all but the final instar, parasitizing equal numbers of hosts in the first three instars (Table I). In the laboratory, the parasite also oviposited in final-instar larvae when confined with them in a rearing cage.

The female of this ichneumonid walks rapidly over the plant, using her antennae to locate the host larva. Oviposition is very rapid once a suitable host has been found. The abdomen is flexed beneath the thorax and between the legs and the ovipositor is thrust quickly into the larva. Egg-laying occupies no more than a second or two. There is no poison sack associated with the ovipositor; hence paralysis does not occur and many larvae, particularly those in the late instars, escape the female by thrashing about violently.

Presence of the parasite arrests pupation of the host. In the laboratory, at 70° F., the parasite developed from egg to adult in 15.5 days when the egg was placed in second-instar larvae. When the egg was placed in fourth-instar larvae, development required only 9.5 days. The parasite emerged from the prepupa one or two hours after the host had formed its cocoon. The parasite then spun its own cocoon within that of the host in three to six hours. In doing so, the parasite pushed the host remnants to the bottom of the host cocoon.

Mating lasts from four seconds to four minutes, there being considerable prenuptial activity. In the laboratory, haploid parthenogenesis frequently occurs, unmated females producing only male offspring. In cultures of *H. insularis* the ratio of males to females was extremely high, about 10:1; however, in the field, based on 1900 reared adults, the sex ratio was 1.1:1.0.

The parasite has four to six generations a year, the number corresponding to that of its host. It hibernates as a pupa, in the cocoon of its host, amongst the remnants of the crop.

H. insularis has not been previously reported from the Transition zone of North America (Muesbeck *et al.*, 1951; Krombein *et al.*, 1958). It occurs in eastern North America west to the 100th meridian, and also in S. California, Mexico, and Hawaii. A closely related species, *H. fenestralis* (Holm.), has been recorded as a parasite of the diamondback moth in many parts of Europe and Asia. *Angitia* (= *Horogenes*) *plutellae* (Vier.) was reported from the moth in Arizona and Colorado (Marsh, 1917), Utah (Knowlton and Jaynes, 1930), Saskatchewan (King, 1929), and Virginia (Poos, 1928).

Microplitis plutellae (Meus.).—This braconid was present in significant numbers during three of the five years. It is a primary parasite of the diamondback moth, attacking second- and third-instar larvae (Table I). The mature parasite larva emerges from the membranous area between the fourth and fifth abdominal tergites of the final instar host and spins its capsule-shaped cocoon on the cabbage plant a short distance from the dying caterpillar. The host larva dies within 24 hours.

M. plutellae was first collected at Merivale in 1953. Muesebeck *et al.* (1951) listed the insect only from Iowa, Colorado, Idaho, and California. However, it has since been identified from Utah, South Carolina, and New York (Krombein *et al.*, 1958).

The abundance of the parasite at Merivale as indicated by fortnightly counts of cocoons on late cabbage was as follows:

Year	Mature *P. maculipennis* larvae	*M. plutella* cocoons	Percentage parasitized
1954	5984	78	1.3
1955	8145	350	4.3
1956	2501	54	2.1

Campoletis sp.—A single specimen of this ichneumonid was reared from a final-instar caterpillar in early June, 1955. The parasite spun its cocoon on the cabbage leaf a short distance from the dying host. This is the first Nearctic host record for the genus. *Sagaritis* (= *Campoletis*) *latrator* (Grav.) has been recorded as a parasite of the diamondback moth in Russia (Thompson, 1957).

TABLE II
Parasites reared from cocoons of the diamondback moth at Merivale, Ont., 1952 - 1956

Year	Number of cocoons collected	*H. insularis*	*D. plutellae*	*G. tenellus*	*D. cavus*	*E. viridescens*	*T. sokolowskii*	*Habrocytus sp.*	*S. albifrons*
1952	1208	581	150	0	0	0	8	0	0
1953	1894	591	350	4	8	9	0	4	0
1954	1465	560	236	0	0	4	0	0	0
1955	1326	305	162	0	0	0	0	1	2
1956	1043	404	227	3	1	0	0	0	0
Total	6936	2441	1125	7	9	13	8	5	2

Parasites Reared from Cocoons

Including *H. insularis*, a total of eight species of parasites were reared from cocoons collected at Merivale (Table II). All but one or two of these were primary; all were internal parasites and all caused death of the host.

Diadromus plutellae (Ashm.).—This ichneumonid was the most abundant pupal parasite at Merivale (Table II). It was present each year from early June until late October, although its numbers were low during the latter month. The females readily attack both prepupae and pupae. Unlike *H. insularis*, presence of the parasite does not inhibit pupation of the host. On encountering a host, the female crawls over the cocoon and examines it with her antennae. She then flexes her abdomen and, inserting her ovipositor through the opening at one end of the cocoon, drives it into the host. Lloyd (1940) found that the presence of the cocoon surrounding the prepupa or pupa of *D. collaris* is important in the acceptance and parasitization of a particular host. Based on 300 adult parasites reared from field-collected cocoons, the ratio of males to females in *D. plutellae* was 0.9:1.0.

The species is transcontinental in the Transition zone of North America (Muesebeck *et al.*, 1951). Members of the genus have been reported as parasites of the diamondback moth in England (Hardy, 1938), Holland (Lloyd, 1940), Finland (Kanervo, 1936), New Zealand (Robertson, 1939), and Russia (Romanova, 1930; Telenga, 1929).

Dibrachys cavus (Wlkr.).—This pteromalid is found throughout eastern North America. It is extremely polyphagous, having been recorded from more than 90 hosts (Muesebeck *et al.*, 1951). *P. maculipennis* constitutes a further host record for the parasite. All nine specimens shown in Table II were reared from cocoons of the diamondback moth collected late in the fall. An additional six specimens were reared from overwintered cocoons collected at Merivale in the spring of 1953. One to three parasites emerged from a single host.

Habrocytus sp., near *phycidis* Ashm.—*H. phycidis*, a polyphagous pteromalid, is found throughout eastern North America. This constitutes a new Nearctic host record for the genus.

Tetrastichus sokolowskii Kurdj.—This eulophid is a parasite of the diamondback moth in Europe and Asia. Ullyett (1947) recorded a species of *Tetrastichus* believed to be *sokolowskii* from the diamondback moth in South Africa. All eight specimens shown in Table II were reared from host cocoons collected late in the fall. An additional 17 specimens were reared from overwintered cocoons collected at Merivale in 1953. The species was first recorded from the Nearctic region in 1953 (Harcourt, 1953). It has since been identified as a parasite of the diamondback moth in New York (Krombein *et al.*, 1958).

Spilochalcis albifrons (Walsh).—This polyphagous chalcid is found throughout the United States and in parts of Canada. It is a primary parasite of the diamondback moth.

Eupteromalus viridescens (Walsh).—This pteromalid attacks the prepupa and pupa of *H. insularis*, and was reared from diamondback moth cocoons collected in the late fall. Robertson (1948) recorded a species of *Eupteromalus* as a hyperparasite attacking *Angitia* (= *Horogenes*) *cerophaga* (Grav.) in New Zealand. This is the first Canadian record for the species.

Gelis tenellus (Say).—This polyphagous ichneumonid is transcontinental in the Austral region of North America. This constitutes a new host association for the parasite. It apparently attacks both *P. maculipennis* and *H. insularis*.

Predators

The following predators of *P. maculipennis* are recorded in the literature: *Larvae*: Vespidae, Chrysopidae, Hemerobiidae, Anthocoridae, and spiders (Ullyett, 1947); Mantidae (Gunn, 1917); Miridae (Kanervo, 1936); birds (Theobald, 1926; Ullyett, 1947; Kanervo, 1936); Syrphidae (Muggeridge, 1930; Ullyett, 1947). *Pupae*: Staphylinidae (Ullyett, 1947); birds (Hardy, 1938; Ullyett, 1947). No predators of the egg are listed.

At Merivale, a mirid nymph was on one occasion observed to attack an egg mass of the diamondback moth, sucking out the contents of several eggs. A small red mite, determined by Dr. H. H. J. Nesbitt, Carleton University, Ottawa, as an erythraeid, ate the eggs in a field study cage.

Spiders, and aphid lions, *Chrysopa* spp., occasionally fed on early-instar larvae in the field. An immature form of the mite *Anystis* sp. (determined by Dr. Nesbitt) was on one occasion observed to carry off a first-instar larvae. Birds periodically landed on the plants in search of larvae; most frequently recorded were the brown-headed cowbird, *Molothrus ater*, the song sparrow, *Melospiza melodia*, and the redwing, *Agelaius phoeniceus*. The last was most common in the early fall, when it descended upon the plots in large swarms.

Cocoons containing prepupae were occasionally destroyed by *Chrysopa* larvae. Birds searching for larvae on the plants ate cocoons as well.

Disease

At Merivale, deaths due to disease were negligible. A fungus, *Entomophthora sphaerosperma* Fres., has been an important factor in reducing field populations of the insect in New Zealand (Cunningham, 1927; Robertson, 1938), South Africa (Ullyett and Schonken, 1940), and Finland (Kanervo, 1946). On the other hand, natural populations of the insect were reported to be comparatively free from disease in England (Hardy, 1938) and the United States (Marsh, 1917). A bacterium, *Bacillus thuringiensis* Berl., has been recently found to be pathogenic to the insect in the laboratory (Tanada, 1956).

Degree of Parasitism by Principal Parasites

Table III indicates that *H. insularis* and *D. plutellae* are less important in regulating populations of the diamondback moth than suggested by accounts of the host in the North American literature. On the average, the two species destroyed slightly more than half of the host population. However, during the near-outbreak year of 1955, they parasitized only about one-third of the host population. This amounted to roughly the same number of cocoons as they destroyed in 1954, despite an 80 per cent increase in abundance of the host.

TABLE III

Numbers of the diamondback moth killed by its two principal parasites in relation to host density, Merivale, Ont., 1952 - 1956

Year	Number of cocoons collected	Percentage parasitized			Number of cocoons per plant
		H. insularis	*D. plutellae*	Total	
1952	1208	48.1	12.4	60.5	4.4
1953	1894	31.2	18.5	49.7	9.9
1954	1465	38.2	16.1	54.3	13.2
1955	1326	23.0	12.2	35.2	22.4
1956	1043	38.7	21.8	60.5	6.0
	6936	35.8	16.2	52.0	11.2

At Merivale, it was not uncommon to find hosts containing immature stages of both *H. insularis* and *D. plutellae*. Fig. 1 shows that numbers of the two species bore a definite relationship. Although *H. insularis* was invariably responsible for most of the total parasitism, at times the curve for parasitism by this species departs markedly from the curve of total parasitism. The curve for *D. plutellae* follows many of these departures very closely. It is interesting that this phenomenon occurred less frequently in 1954 and 1955, when density of the host was relatively high. Given the opportunity to examine many more hosts per unit area in those two years, females of *D. plutellae* apparently avoided ovipositing in prepupae containing *H. insularis*. Lloyd (1940) observed similar discrimination by *D. collaris* in the laboratory.

Discussion

It was not within the scope of the present study to establish the efficacy of *H. insularis* or *D. plutellae*, or of any of the other entomophagous species that attack the diamondback moth. These data await the completion of life-table studies begun by the writer in 1958. The check exercised by parasites on the population of a given insect is but one of many mortality factors in the population and is influenced by the interaction of the parasites with the other mortality factors present. At best, periodic field collections of cocoons as in the present study yield only data on "apparent mortality" because, as is pointed out by Miller (1955), removal of host cocoons interferes with the natural course of events and there is no way of knowing how many parasitized individuals might actually be destroyed by other mortality factors before the parasites emerge. In other words, some cocoons, although parasitized, may actually be destroyed by agents other than parasites.

Early workers in the field of population ecology believed that parasite populations fluctuate in direct proportion with density of the host, and its corollary, that the number of hosts attacked is a linear function of the number of parasites was also widely accepted. More recently, laboratory experiments of several workers, e.g., DeBach and Smith (1941), Burnett (1951), and Ullyett (1949a, b) have shown that the number of hosts attacked by a fixed population of parasites increase at a diminishing rate with increasing host density. The same authors (DeBach and Smith, 1947; Burnett, 1958; Ullyett, 1949a, b) further point

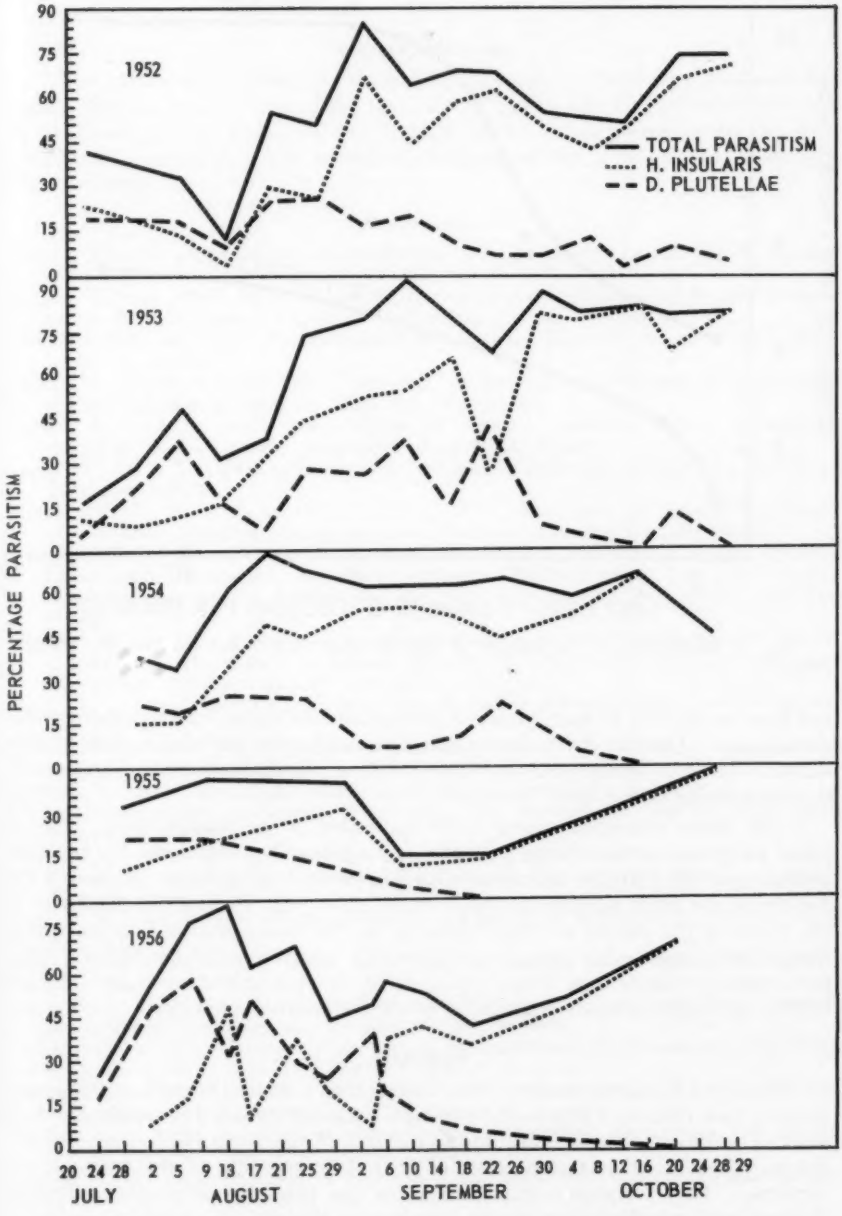

Fig. 1. Parasitism of *P. maculipennis* cocoons by *H. insularis* and *D. plutellae*, Merivale, Ontario, 1952-1956.

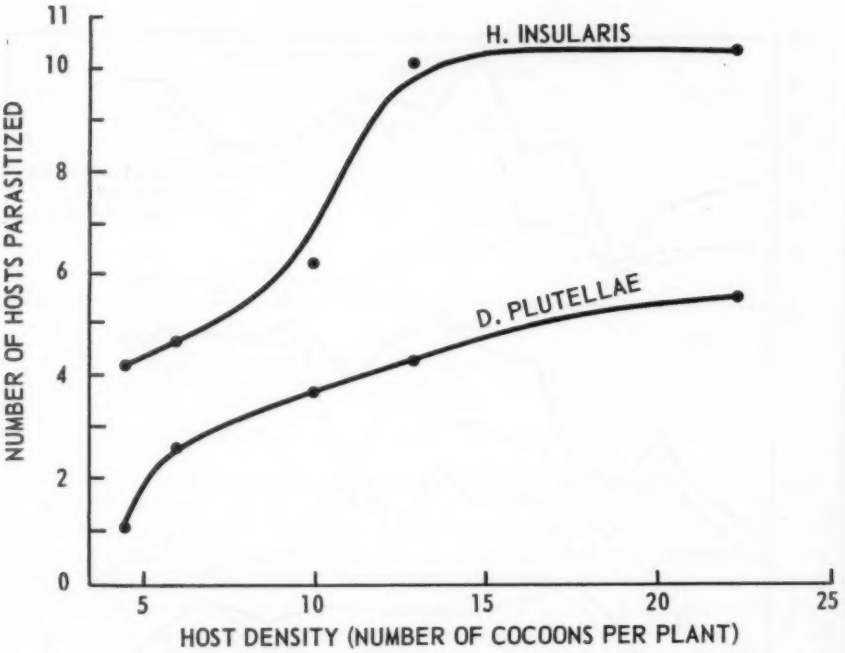

Fig. 2. Relationship of the number of hosts attacked to host density, Merivale, Ontario, 1952-1956.

out that the number of hosts attacked per parasite decreases with increasing parasite density. The fact that parasites become less effective per head as their density increases has been interpreted by Watt (1959) as a built-in mechanism to prevent the annihilation of the hosts, their food.

The above principles appear to be applicable in the present study. Fig. 2, based on yearly totals, shows that the rate of attack at Merivale by both *H. insularis* and *D. plutellae* decreased with increasing host density. Although the density of the adult parasites probably varied from year to year, the similarity in the form of the curves to those obtained in the above studies is noteworthy. Similar behaviour under natural conditions has been recorded by Miller (1959) for *Apanteles fumiferanae* Vier., a parasite of the spruce budworm, and Holling (1959) for small mammalian predators of the European pine sawfly.

Summary

During a five-year study of the diamondback moth, *Plutella maculipennis* (Curt.), near Ottawa, Ontario, the principal parasites recorded in permanent field plots were the ichneumonids *Horogenes insularis* (Cress.) and *Diadromus plutellae* Ashm., which destroyed an average of 36 and 16 per cent of the cocoons respectively. Less frequently recorded were the braconid *Microplitis plutellae* (Mues.), the eulophid *Tetrastichus sokolowskii* Kurdj., the chalcid *Spilochalcis albifrons* (Walsh), the ichneumonids *Gelis tenellus* (Say) and *Campoletis* sp., and the pteromalids *Dibrachys cavus* (Wlkr.), *Habrocytus* sp., near *phycidis* Ashm., and *Eupteromalus viridescens* (Walsh), the last being a parasite of *H. insularis*. Predators recorded included birds, mites, spiders, Chrysopidae, and a

mirid larva. Deaths due to disease were negligible. Population relationships are discussed.

Acknowledgments

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Distribution of *Xenopsylla cheopis* (Rothsch.) (Siphonaptera: Pulicidae) in Canada

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Of the many species of fleas incriminated in plague transmission, the most notorious is the oriental rat flea, *Xenopsylla cheopis* (Rothsch.). This is due to its early discovery as a plague vector (Simond, 1898), its demonstrated superior ability to transmit the infection (Kartman and Prince, 1956), and its recognition as the principal vector of plague from rat to man. Holland (1949) regards its presence in any geographical area as a matter of concern.

During the past two years we have been carrying out a rodent disease survey in communities along the St. Lawrence River from Kingston, Ontario, to Montreal, P.Q. Collections also have been made in Saint John, New Brunswick, and in Halifax, Nova Scotia. An integral part of this survey has been the collection and identification of such ectoparasites as may be found on the rodents under study. One result has been the discovery of two new distribution records for *X. cheopis*.

The occurrence of *X. cheopis* in Canada was first reported by Holland (1940) from Vancouver and New Westminster, British Columbia. It was found commonly on rats on garbage dumps but rarely, or not at all, on rats collected along the waterfront. Its prevalence on garbage dumps was attributed to the relatively high temperature and humidity found in rat burrows in the vicinity of decomposing garbage. Subsequent surveys in the British Columbia coastal region indicated a decline in the *cheopis* population (Holland, 1949). Kuitunen-Ekbaum and Webster (1947), in a report on the incidence of trichinosis in rats in Toronto, mentioned having found *X. cheopis* as commonly as the European rat flea, *Nosopsyllus fasciatus* (Bosc.). The only other Canadian record of *X. cheopis* known to the writers is contained in the files of the Laboratory of Hygiene. Four of 181 fleas collected from 272 rats in Halifax, by J. B. Poole in 1942 and identified by W. E. Whitehead, Macdonald College, Quebec, were *X. cheopis*.

During the first three weeks of June, 1958, 60 *Rattus norvegicus* were live-trapped or shot on a dump in Cornwall, Ontario, without yielding a single ectoparasite. At that time the dump was heavily infested with rats. During the first week in July, dumping of household and restaurant garbage at this location was discontinued and at the same time an extensive and effective rat-control program was carried out. On 29 July, 11 rats were live-trapped and from these, 20 *X. cheopis* were collected, six males, 14 females.

Our second collection of this species was made in Montreal in 1959. From 18 June to 14 July, 80 *R. norvegicus* were live-trapped inside buildings in various parts of the city. Twenty-one of these rats collected in the basement of a restaurant yielded three *X. cheopis* females.

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Oviposition of the Red-Headed Pine Sawfly, *Neodiprion lecontei* (Fitch)[1]

By K. J. GRIFFITHS[2]

Introduction

The oviposition behaviour of *Neodiprion* sawflies has been the subject of much investigation in recent years. The impetus for this interest seems to lie in the paper by Atwood and Peck (1943), in which it was suggested that the number and spacing of eggs on needles were a useful tool for the identification of members of this important group of conifer defoliators. Ghent (1955) has analysed the egg clusters of *N. pratti banksianae* Roh., and Ghent and Wallace (1958) have investigated the behaviour responsible for the pairing of eggs on adjacent jack pine (*Pinus banksiana* Lamb.) needles by *N. swainei* Midd. More recently, Ghent (1959) has presented a study of the factors determining the spacing of eggs by the European pine sawfly, *N. sertifer* (Geoff.). Of these, the 1955 and 1959 papers, in addition to making valuable contributions to our understanding of the behaviour of adults, cast doubt on the usefulness of the number and spacing of eggs as identifying characters in these species.

The present paper combines the methods employed by Ghent (1955) for *N. p. banksianae* and by Ghent (1959) for *N. sertifer* in order to determine whether there is justification for the continued use of egg number and spacing as an identifying character in *N. lecontei* (Fitch), and whether it can be inferred from measurement of the appropriate variables only that the patterns of oviposition behaviour found to exist in *N. sertifer* by Ghent (1959) also exist in *N. lecontei.*

N. lecontei is an appropriate species to form the next step in this series of investigations on sawfly oviposition patterns. According to Ross (1955), it belongs to a different phylogenetic complex from the previously investigated species *N. p. banksianae*, *N. swainei* and *N. sertifer.* Ecologically, however, it resembles *N. swainei* in its seasonal history, since both species normally overwinter in the cocoon and undergo larval development in the late summer and fall. Further, it resembles both *N. p. banksianae* and *N. sertifer* in its oviposition habits, belonging to that group designated by Ghent (1959) as Type 3, i.e., those that lay a row of regularly spaced egg pockets on the mature needles of various pines.

Methods and Materials

The egg clusters used in this study were obtained from an outbreak of *N. lecontei* on red pine, *Pinus resinosa* Ait., in the Kirkwood Forest Management Unit, north of Thessalon, Ont., in 1956. They were collected shortly after oviposition from a plantation of four-to-six-foot trees on which the population of *N. lecontei* averaged 0.19 clusters per tree.

Egg-bearing needles were measured and the number of eggs per needle counted in 58 clusters immediately after collection. Later, measurements of the width of needles and the area occupied by eggs in 40 of these clusters were also made. Since it is generally believed that a single egg cluster represents the work of a single female, and since it was known that considerable variation in the size of females exists, variability in egg number and spacing caused by differences in female size was contained in known units by utilizing only cluster averages in all calculations.

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Results

As has been shown previously (Griffiths, 1958), *N. lecontei* adults prefer open-grown trees over shaded trees for oviposition, and among open-grown trees, some of them are more susceptible to attack than others. This susceptibility remains from year to year. Adults also exhibit a preference for ovipositing at the tips of twigs. In the material under study egg clusters were found only on the previous year's foliage, and 87.5 per cent of them were in the apical third of this foliage, with the remainder in the middle third. No clusters were found in the basal third of the shoot.

The number of eggs laid in a single cluster averaged 119.49 $\pm$ 6.72. A statistical comparison of egg cluster size in 1956 with that found in 1955 in the same area showed that egg cluster size was not significantly different in the two years. Benjamin (1955) reported an average of 116 eggs per cluster on red pine in Michigan, essentially the same as that obtained in the present study.

When the distribution of eggs within single needle bundles was examined, it was found that 404, or 74.7 per cent of the 541 egg-bearing bundles examined had eggs on one of the needles only. Of the 137 bundles on which eggs were laid in both needles, 32.8 per cent were laid on the adjacent edges of each needle, and 67.2 per cent on opposite edges. Only 10 needles, or 1.5 per cent of the 678 egg-bearing needles examined, had eggs on both edges of the same needle.

Egg number in relation to needle length

In the egg clusters examined the number of eggs per needle ranged from one to 38, with an average of 14.1 $\pm$ 0.36. However, it was found that the number of eggs laid in a single needle could not be considered an intrinsically determined specific character. Plotting the average number of eggs per needle in each of 58 clusters against the average length of egg-bearing needles in these clusters (Fig. 1) showed a definite tendency for more eggs to be deposited on long than on short needles. Calculation of a correlation coefficient for these data showed that this tendency was statistically real, a correlation coefficient of + .576 $\pm$ .088 being obtained, which, with 56 degrees of freedom, is significantly well beyond the .01 level.

Egg spacing in relation to needle width

Ghent (1959) described the pattern of leg movements involved in the cutting of a row of egg slits by a *N. sertifer* female. He observed that the grip points of the legs were on the opposite side of the needle to that in which the egg slits were being cut, and that the metathoracic legs were fully extended backward during the process. He deduced from this that the thickness of the needle must affect the spacing between eggs. Later in the same paper he confirmed this supposition by showing a strong correlation between needle width and egg spacing (expressed as the length of needle occupied by one egg and one space) on all three host tree species on which *N. sertifer* was found.

Similar measurements were made on red pine needles bearing *N. lecontei* eggs, and a relation was also found to exist between them (Fig. 2). The correlation coefficient for this relation is — .338 $\pm$ .140 (degrees of freedom 38, $p = .03$).

Although no observations were made on the movements of legs of *N. lecontei* during the egg-laying process, those made by Ghent (1959) on *N. sertifer* indicated that the length of the fully-stretched metathoracic leg may play an equally important role for oviposition in *N. lecontei*. Therefore, some discussion of the relation between leg length and needle width is pertinent here.

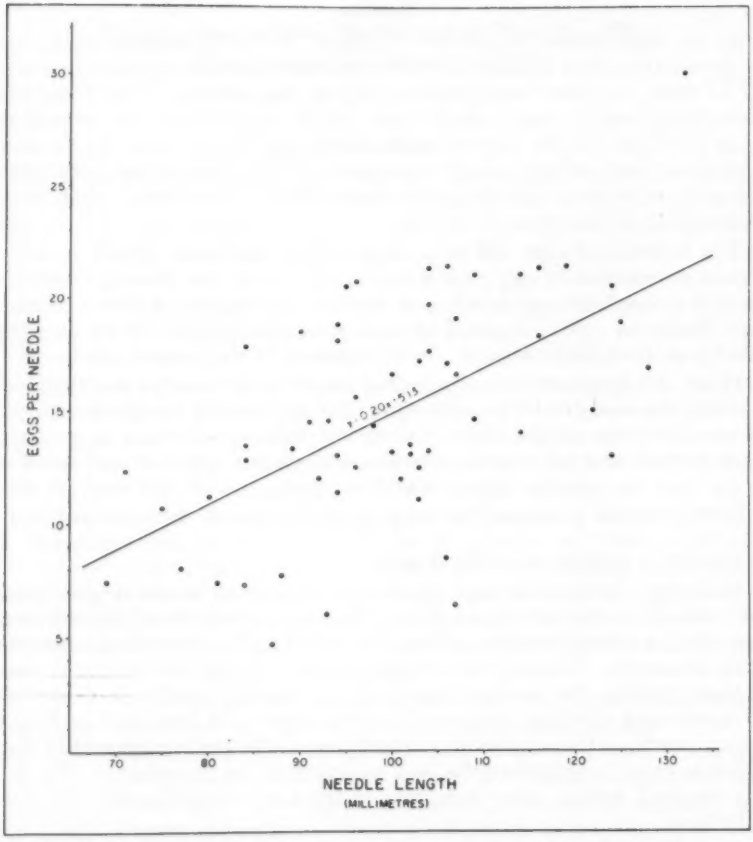

Fig. 1. Correlation diagram; eggs per needle vs. needle width. Each point represents the average number of eggs per needle in one cluster plotted against the average length of egg-bearing needles in that cluster. $r_{x.y} = + .576 \pm .088$.

In the egg-slit cutting process, the width of the needle and the length of the metathoracic leg may be considered as forming two sides of a right angled triangle, the shortest side being needle width and the hypotenuse leg length. It is a simple matter to calculate the length of the third side of the triangle, which is the distance along the needle between the attachment of the leg to the metathorax and its grip point on the needle. Some constant proportion of this calculated length is the distance between eggs, the exact proportion depending on the length of the egg slit, the distance of the metathoracic leg attachment from the saw, and the number of movements made by the legs between the cutting of each egg slit.

Measurements were made of the lengths of the metathoracic legs of 48 females obtained in the same plantation and same year as the egg clusters were collected. These lengths ranged from 5.83 mm. to 7.48 mm. with a mean of 6.82 ± 0.051. Widths of individual egg-bearing needles ranged from 0.900 mm. to 1.485 mm., with a mean of 1.200 ± 0.0053. Calculations of the unknown third side of the triangle mentioned above were made, using the longest leg measure-

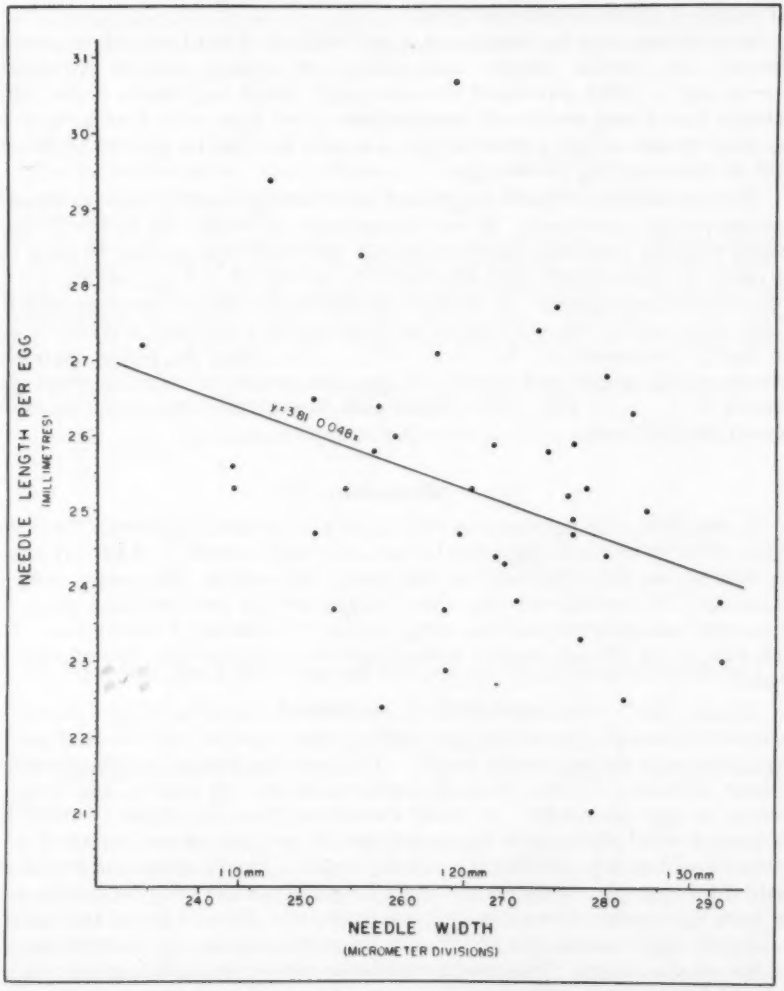

Fig. 2. Correlation diagram; needle length per egg vs. needle width. Each point represents the average length of needle occupied by one egg and one space in one cluster plotted against the average width of egg-bearing needles in that cluster. $r_{x,y} = -.338 \pm .140$.

ment with the narrowest needle sampled and the shortest leg measurement with the widest needle. These give the two extremes of distances to be expected and the ratio between them was calculated as 1.32. The actual ratio of greatest spacing between eggs to smallest spacing between eggs found in egg clusters was 1.46, not greatly different from the calculated ratio. The difference is in the direction which would be expected if the movements of the legs were of a more complicated type than that envisaged in the simple triangle above, if for instance, two steps were taken between each oviposition (as is the case in *N. sertifer* (Ghent, 1959).

Interaction of needle length and width

It is obvious that the number of eggs found on a needle is affected simultaneously by needle length and width. A strong positive correlation ($r = +.610 \pm .099$) was found between needle length and needle width, which indicates that a long needle will tend to have more eggs on it than a short one not only because of its greater length, but also because its greater width will result in closer spacing of the eggs.

The interactions of needle length and width on egg number have been studied by using partial correlations. It was not necessary to utilize this statistical tool in dealing with the correlation between needle width and egg spacing because here the effect of needle length was eliminated by the use of average spacing per egg in the original calculations. In order to obtain the correlations between each pair of the three variates the correlation between needle width and number of eggs per needle was calculated. It was $+ .419 \pm .130$. Then the partial correlation between needle length and number of eggs per needle with needle width kept constant is $r_{13.2} = + .444 \pm .129$, which with 39 degrees of freedom is significant beyond the .01 level.

Discussion

In describing the egg patterns of *N. lecontei*, Atwood and Peck (1943) state "from 10 to 30 or more eggs may be laid on a single needle." The majority of egg-bearing needles examined in this study fell within this range, but, approximately 36 per cent bore less than 10 eggs and five per cent bore more than 30, so that variations beyond this range cannot be considered uncommon. Further, nine of the 58 egg clusters studied had an *average* of less than 10 eggs per needle.

Ghent (1955), working with *N. p. banksianae*, found that 40 per cent of the variation in average egg number per needle in that species could be attributed to correlation with average needle length. This is on the basis of simple correlation, without allowance for the effect of needle width on egg spacing and hence on number of eggs per needle. A similar calculation from the simple correlation in the present work shows that approximately 33 per cent of the variation in *N. lecontei* could thus be attributed to needle length. Furthermore, the partial correlation for eggs per needle versus needle length, when the effect of needle width has been eliminated, shows that only approximately 20 per cent of the variation in average egg number per needle can be accounted for by correlation with average needle length. This lower correlation can be attributed, at least in part, to the difference in length of needles on the two host trees on which these sawflies oviposit. Red pine needles can range up to five or more times the length of jack pine needles, so that the process of oviposition on any one needle occupies more time on red than on jack pine. Thus, there is a greater chance that the female will be interrupted during the oviposition process, by attempted predation or by the onset of unfavourable physical conditions. Any such interruption will lessen the number of eggs laid on a single needle, which will tend to decrease the correlation with needle length.

The existence of a correlation between egg spacing and needle width strongly suggests that, in the egg-slit cutting process, *N. lecontei* behaves in a manner similar to that found in *N. sertifer* by Ghent (1959). Actual observation of this process in *N. lecontei* is justified by these results, and such work on this and other closely-related sawflies will be of help in the continuing study of the phylogenetic relations of the diprionid sawflies.

Acknowledgments

I would like to indicate my appreciation of the interest in and assistance with this study given by A. W. Ghent. The manuscript has also profited by the comments of R. M. Belyea and other colleagues.

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(Received January 8, 1960)

Note on the Lectotype of *Chrysops wiedemanni* Kröber (Diptera : Tabanidae)

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In his treatment of *Chrysops wiedemanni* Kröber, Philip (1959, pp. 203-4) stated, "Syntypes in Hamburg were casualties in the war, but one intact syntype female remaining in the Canadian National Collection is available as lectotype." Later, Philip (*in litt.* Jan. 19, 1960) explained, "my wording was ambiguous about the lectotype of *Chrysops wiedemanni*. I indicated its availability in contrast to the loss of all other syntypes in Hamburg but this was intended to officially designate your specimen as lectotype and it should be so labelled".

This note is to confirm that the syntype in the Canadian National Collection (C.N.C. Paratype no. 2493) is the lectotype of the species and has been labelled accordingly.

Reference

Philip, Cornelius B. 1959. New North American Tabanidae. X. Notes on Synonymy, and descriptions of a new species of *Chrysops*. *Trans. Amer. Ent. Soc.* 85: 193-217.

(Received March 11, 1960)

A New Species of *Microctonus* (Hymenoptera: Braconidae)

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C. C. Loan, of the Entomology Research Institute for Biological Control, Belleville, Ontario, has recently reared from a native *Sitona* weevil a new species of *Microctonus* Wesmael.

***Microctonus sitonae* new species**

This species keys to *eleodis* Vier. in Muesebeck's revision (U.S. Dept. Agric., Misc. Pub. No. 241, p. 16, 1936) and is very similar to that species and *M. aethiops* Nees. The female of *M. eleodis* differs in having a longer ovipositor sheath (about 1.2 times as long as abdomen beyond petiole), shorter petiole (only 1.9 to 2.2 times as long as its apical width), less strongly excavated and longer propodeum (only about 1.5 times as wide as long). The female of *M. aethiops* differs in having a pair of small dorsal pits near the middle of the petiole (both sexes), shorter ovipositor sheath (about 0.75 times as long as abdomen beyond petiole), slightly shorter petiole (about 2.2 times as long as apical width), and completely black petiole.

Holotype, ♀.—Length (excluding ovipositor) 3 mm. Head transverse, slightly broader than thorax; temple 0.8 times as wide as eye; face 1.2 times as wide as long from antennal sockets to base of clypeus; malar space about as long as basal width of mandible; occipital carina well developed, but weaker above and only very vaguely indicated for a short interval medially; face and clypeus alutaceous and finely pubescent, rest of head smooth and shiny with sparse, fine punctures. Antennal flagellum 22-segmented, about as long as body. Ocelli in a flat triangle, small, greatest width of lateral ocellus 0.45 times ocell-ocular space.

Mesonotum shiny, shallowly punctate, and moderately hairy, but lateral lobes mostly shining, impunctate and glabrous behind; notauli complete, deep, and foveolate; area of convergence large, rugulo-punctate, with a weak irregular median carina; mesopleuron mostly shining and sparsely, irregularly punctate; with a short, broad, diagonal, rugulo-punctate impression below; scutellum shiny, impunctate; metapleuron and propodeum reticulate-rugose, about twice as wide as long, very abruptly declivate and strongly excavated medio-posteriorly.

First abscissa of radius about 0.4 times width of stigma; radial cell slightly less than half as long as stigma measured along wing margin; second abscissa of radius strongly bowed; nervellus almost twice as long as longest marginal cilia of hind wing and a little longer than lower abscissa of basella.

Petiole about 2.5 times as long as its apical width, without any dorsal pits, basal 0.4 smooth, apical 0.6 aciculate; sides of petiole broadly separated below. Remainder of abdomen smooth and shiny, no suture visible between tergites two and three. Ovipositor as long as abdomen; ovipositor sheath slightly shorter than abdomen beyond petiole.

Color reddish testaceous, the following parts black: flagellum except basal two or three joints below, stemmaticum, dorsal surface of thorax (including mesonotum, scutellum and all propodeum), ovipositor sheaths. Stigma and wing veins brown.

Allotype, ♂.—Similar to the holotype except as follows: length 2.5 mm., temple as wide as eye, face about 1.6 times as wide as long, face and clypeus polished and shallowly punctate, antennal flagellum 26-jointed, mesonotum and

mesopleuron less strongly punctate, area of convergence of notauli with an irregular median carina, length of petiole only 2.2 times its apical width.

Color black, the following parts reddish brown: scape below, lower two-thirds of head, all legs and coxae, tegula and wing veins. Extreme base of petiole, and abdomen beyond petiole, dark brown.

Variation.—Females: length 2.2-3 mm.; flagellum 20- to 22-jointed; median carina in area of convergence of notauli strong to very weak; petiole 2.5 to 2.7 times as long as its apical width; base of antennae, upper parts of pronotum, mesopleuron, mesosternum, and petiole centrally, dark brown to black.

Males: length 2-2.5 mm.; flagellum 25- to 27-jointed; median carina in area of convergence of notauli sometimes weak; propodeum sometimes with apical transverse carina vaguely indicated; scape, centre of face, hind coxa basally and above, black. Abdomen beyond petiole black to brown.

Cocoon.—Solitary, oval, white, opaque, with some fine loose silk and attached to the substratum by its side.

Host.—Adults of *Sitona scissifrons* Say (Curculionidae) feeding on *Vicia cracca* Linn.

Specimens seen.—12 ♂ ♂, 8 ♀ ♀.

Holotype: Female, Belleville, Ontario, July 8, 1959, C. C. Loan, reared from *Sitona scissifrons* Say on *Vicia cracca* Linn. (Canadian National Collection No. 7147).

Allotype: Male, same data as holotype (C.N.C.).

Paratypes: ONT., 9 ♂ ♂, 5 ♀ ♀, same data as holotype (C.N.C.); ♂, ♀, same data but June 25, 1959 (C.N.C.); ♂, ♀, Ottawa, June 7, 1939, and May 29, 1941, respectively, O. Peck (C.N.C.).

(Received March 8, 1960)

NOTICE

Tenth Annual Meeting of the Entomological Society of Canada

The 10th Annual Meeting of the Entomological Society of Canada will be held on the University of Saskatchewan campus, Saskatoon, Sask., Sept. 12, 13 and 14, 1960. The invitation speaker will be Dr. K. D. Roeder, of Tufts University, Massachusetts, speaking on The Nervous System and Behaviour. There will be two symposia, one on the comparative physiology of the nervous system in insects and mammals, and the other on speciation. A one and one-half hour period will be devoted to informal discussion groups on various topics under discussion leaders. The equivalent of about three-quarters of one day will be available for submitted papers.

Members of the Society will have received the advance program notice. Others interested in receiving this should inquire of the Secretary, Saskatchewan Entomological Society, Canada Agriculture Research Station, University Sub Post Office, Saskatoon, Sask.

The Need for Direct Observation of Behaviour in Studies of Temperature Effects on Light Reactions[1]

By W. G. WELLINGTON[2]

Introduction

Many insects which are photopositive at moderate temperatures begin to react photonegatively when they are heated sufficiently. If they are returned to lower temperatures, they become photopositive again. This reversible reaction sometimes prevents injury or death in any environment. In extreme environments, it permits some species to live where they could not survive without it. Consequently, a knowledge of the responses involved and the temperatures at which they occur may help investigators to understand otherwise inexplicable changes in the behaviour, numbers, or distribution of natural populations.

From time to time, ecologists in need of such information return to the laboratory to perform the necessary experiments. When they do, they are apt to be less interested in the reaction than in its ecological significance. With this in mind, they tend to choose methods which minimize observations of behaviour but emphasize the temperature range within which reversal takes place. Prominent among such methods are those which depend primarily on intermittent records of the positions of animals in the apparatus. These techniques often seem more objective than any which require decisions concerning behavioural changes, and they also are easier to use when large groups must be employed for quantitative comparisons.

Unfortunately, methods of recording positions without regular reference to the behaviour of the individuals which comprise the group were developed for other purposes than studies of reversal phenomena. Borrowed techniques require critical appraisal before they can be safely applied outside their original field of inquiry, but those applied in reversal studies seem to have escaped examination. This paper shows some consequences of applying such techniques when the ultimate purpose is interpretation of behaviour in natural situations. But first a comment on behaviour associated with reversal will be helpful in subsequent discussions.

The Reaction

In natural situations, photonegative behaviour need not involve concealment in a dark crevice or movement to the darkest location. Instead, it often takes the form of movement to an area of lower light intensity when the more brightly illuminated area becomes too hot.

In laboratory apparatus, more stereotyped reactions may be involved. These are easily demonstrated by confining the insect in a dark-light alternative chamber – an arena with one part shaded so that a sharply defined boundary exists between the dark and light areas. A photopositive animal placed in the dark will cross the boundary without visible reaction and move farther into the lighted part. If it approaches the boundary from the lighted side, however, it often reacts when it reaches the shadow-line and does not cross. Its reaction usually includes a sharp turn back into the light.

When the temperature is raised to the point where the insect reverses its response to light, reactions no longer occur during boundary crossings from the light to the dark sides. Instead, they occur only on the dark side of the line, so that the insect turns back into the shaded area.

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In later pages, all reactions along the boundary that keep the animal on the same side of the line will be called "boundary reactions". The elementary behaviour patterns they contain have much in common with those seen in gradients of other physical factors besides light, and the classification of these patterns has been discussed in detail by Fraenkel and Gunn (3). More recently, Ewer and Bursell (2) suggested amendments to this classification and also proposed the term, "titubant reaction", for some types of "shock reaction" at boundaries. Nevertheless, the general term, "boundary reaction", is sufficiently clear for present purposes.

In any study of behaviour in a dark-light chamber, boundary reactions provide the only real basis for decisions concerning the photic orientation of an animal. When the animal is photopositive, it reacts only on the lighted side of the line. As soon as it becomes photonegative, it reacts only on the dark side. And its reversal temperature is that at which it stops reacting on one side of the boundary and begins to react on the other. Since this is the ecologically significant temperature we seek, we should compare its determination by this direct method with results obtained by methods which discount behaviour.

Sources of Error in the Collection and Interpretation of Position Records

Present methods of recording and interpreting the positions of animals in dark-light chambers have been borrowed more or less intact from earlier studies of the behavioural changes of animals confined in humidity chambers. While the original methods were being refined, various formulae to express the intensity of the humidity reactions observed became attached to them. For example, Gunn and Cosway (4) used $\frac{100\ (D-W)}{D+W}$ to portray shifts in numbers from one side of the chamber to the other (see also (7)). D and W represent the numbers counted on the dry and moist sides of the chamber, respectively, and conversion of the index to a percentage reveals the intensity of reaction by showing the *excess* percentage maintained on the drier side.

Humidity alternative chambers have a central zone where the test pair of humidities mix to some extent, however, and this zone often contains some of the animals when records are taken. The formula above neglects these animals, but Bentley (1) revised it to include them by using $\frac{100\ (D-W)}{N}$. N is the total number of test animals, but the index still expresses the excess percentage on one side of the chamber. Its values range between $\pm$ 100, and zero values arise when equal numbers occur on both sides. This implies no difference in response to the pair of moisture levels used in the test.

Bentley's version is the one most frequently employed when the positions of animals in dark-light chambers are recorded during studies of reversal (e.g., 5, 6, 8). It then becomes $\frac{100\ (L-D)}{N}$, with L and D representing the numbers of animals in the light and dark portions of the chamber, respectively.

With either humidity or light, the index appears to provide an objective means of assessing reaction intensity in large groups, since it requires only an accumulation of position records instead of decisions concerning individual changes in response. It is not really applicable to light-reaction reversal problems, however. Some aspects of light reactions may be similar to humidity

reactions, but dark-light alternative chambers only superficially resemble humidity alternative chambers, and different events occur within them. For one thing, the boundary between light and dark is much sharper than that between any pair of differing humidities. For another, activity levels of animals under test in a dark-light chamber are influenced not only by moisture and by differences in light intensity but also by rising or falling temperature. The combination of sharp boundary and highly variable activity in a *confined* space has consequences which destroy the utility of position records and their accompanying indices.

The investigator soon learns to make dark-light alternative chambers small in relation to the size of the animals they confine. If he provides them with too great an expanse to cross rapidly, animals in the centre of a light or dark area may stop because of heat stroke or cold trapping at extreme temperatures before they reach the dividing boundary. Since the record lost in such cases is precisely the one required, small areas are the rule so that boundary contacts can be frequent and rapid.

When animals are sluggish, this raises no special problem, because they tend to remain in one area until they become uncomfortable enough to move to the alternative light intensity. When they are very active, however, they encounter the boundary frequently in their travels. Since the boundary is sharp and distinct, they generally react to it in the expected way, but whether or not they detect it depends on their ability to discriminate between light and dark at the speed and angle at which they encounter it. In practice, many rapidly moving insects often overshoot the boundary without reacting and enter an area to which their responses alone would not have led them. This is clear enough to anyone watching their behaviour before and after they cross. It is not revealed, however, by simple periodic records of their positions, so that any index based on such records may be very misleading. Let us examine the consequences of different activity levels and rates of travel in a confined space in more detail.

Examples

When larvae of the arctiid, *Halisidota argentata* Pack., are removed from their food and confined in a featureless arena, they exhibit well-marked alternating bursts of activity and quiescence. Whether extremely active or relatively quiet, they are photopositive at 20° C., travelling to the brightest area available when they are released on a light-board. When they are confined in a dark-light chamber at this temperature, however, their variable activity may produce anomalous results if their positions are recorded without reference to their behaviour. The effects of these changes in activity can be shown best by comparing the *motion* of larvae confined in a uniformly illuminated chamber with the *numbers* observed in the lighted half of a dark-light chamber. The tabulations below show the effects of variable activity when 12 eighth-instar larvae were compared in this way.

The larvae averaged approximately 2.5 cm. in length. The arena had a diameter of 15 cm. The nylon platform on which the larvae were placed was mounted 2 cm. below the top of their container, which was sealed with a plate-glass lid. Illumination came from a centrally-placed overhead light source, and amounted to 20 foot-candles at the surface of the platform. This apparatus was a standard dark-light alternative chamber described in earlier work (10) and used throughout the experiments reported here. In the first series of observations, however, the mask for the light source was removed, so that the whole platform was flooded with light of uniform intensity, and there were no shadows around

TABLE I

The numbers of motionless *H. argentata* larvae in a uniformly lit chamber compared with the numbers counted in the illuminated half of a dark-light alternative chamber (T = 20°C. in each test).

	Hour No.											*n*
	1	2	3	4	5	6	7	8	9	10	11	
No. motionless in uniform light:	6	4	3	5	9	5	11	8	10	12	12	*12*
No. in lighted half:	6	4	4	6	9	6	9	9	8	12	12	*12*

the edges of the arena. The temperature of the container remained at 20° C. throughout this and the next series of observations.

Hourly counts of motionless larvae gave the numbers in the first row of Table I. The records show that activity in uniform light increased during the first three hours of confinement, then decreased somewhat erratically until the last two hours, when it ceased altogether.

The larvae were given food overnight, then returned to the arena on the following day so that the observations could be repeated during the same part of the day. This time, however, half the platform was shaded by inserting a black cardboard mask between the lamp and the chamber. Illumination in the lighted half was still 20 foot-candles, but light intensity in the shaded half was too low to measure, so that the shadow-boundary between the two halves was very distinct. Hourly counts of the numbers of larvae in the lighted half of the chamber are shown in the second row of Table I.

The numbers in the lighted half of the chamber showed increases and decreases comparable with the changes in numbers of motionless larvae in uniform light, except between hours 7 and 8, and 8 and 9. It is clear that more larvae were found in the lighted half of the alternative chamber when activity was low than when it was high. And this illustrates a very typical effect of variable activity on results obtained from position records in such a chamber.

It would be a mistake to suppose these data indicate that increased activity results in a decrease in the intensity of photopositive behaviour, or that changes in photic response are in any way associated with changes in activity in this experiment. No such association was involved here. Smaller numbers in the light during periods of increased activity resulted simply from an increased number of crossings into the dark (without boundary reactions) by rapidly moving *photopositive* animals confined in a small space. This was confirmed easily enough by watching the animals while they were in motion. When they approached the boundary at relatively steep angles they detected it and turned back into the illuminated area. But when they approached it rapidly at very shallow angles, or suddenly changed their direction of travel when they encountered another larva near the boundary, they crossed into the dark without reacting and remained there for a time. When they were quieter, they tended to rest in the light or move about in it along devious paths for a few body-lengths.

This explanation depended on observations not normally part of position-record procedure, however, and it is important to note what happens when the intensity index is applied to the alternative-chamber figures in the second row of

Table I. When indices were calculated from the position records for animals in the lighted half of the chamber[3], the percentages[4] shown in the following tabulation were obtained:

Hour:	1	2	3	4	5	6	7	8	9	10	11
Excess % in lighted half:	0	−33	−33	0	+50	0	+50	+50	+33	+100	+100

Unaccompanied by observations of the actual behaviour of the animals, the index values suggest that the group was relatively photonegative during its first three hours in the chamber, and that it did not become consistently photopositive until it had been exposed for some seven hours. In reality, the insects were photopositive at all times.

Advocates of the index are at liberty to point out that exposure of this duration ultimately did reveal the true photopositive response of the insects known to exist at 20° C. It is well to remember, however, that even this demonstration was possible only because activity in the confined space decreased and remained at a low level.

Similar difficulties due to variable activity in confinement arise when temperature changes rapidly. In fact, the greatly increased rates of travel that accompany higher temperatures complicate the situation still further. Before examining records from groups exposed to rising temperature, however, it is instructive to examine the activity and behaviour of individuals at different temperatures in a dark-light chamber. Such information is best obtained by confining an individual for brief periods at different constant temperatures. If the animal is allowed to move freely, its path can be traced and its stops, turns, boundary contacts, and rates of travel can be recorded. This was done for an eighth-instar larva of *H. argentata* (2.5 cm.) and a third-instar larva of the forest tent caterpillar, *Malacosoma disstria* Hbn. (1.2 cm.). The results shown in Tables II and III are typical of what may be expected from other larvae.

The records in the tables were obtained by observing the larvae for successive six-minute periods at four different constant temperatures. Before they were treated in this way, the temperatures at which they became photonegative were determined by observing their boundary reactions while the chamber temperature was slowly rising. Temperature changes were obtained by placing the chamber on a hot-plate warmed by heating coils or by a 200-watt lamp (10). A small amount of water in the base of the container facilitated heating, and its vapour minimized desiccation of the larvae at higher temperatures. The platform temperature was measured with a thermocouple threaded through the nylon.

The *H. argentata* larva reversed its reaction to light at 29.7° C. It was then exposed for six-minute periods at 20.5, 25, 28, and 30° C. The highest temperature was chosen because it was only fractionally above the reversal temperature, thus providing a good illustration of the immediate change in boundary reaction that occurred as soon as reversal took place. The *M. disstria* larva originally reversed at 31.5° C., but its reversal temperature was raised to 36.4° by over-

[3]For these and later index calculations, all animals were recorded as being in the light or in the dark. It was unnecessary to discount those on the border line, because all parts of the chamber were sufficiently visible when the shadow was projected. Animals along the border generally were travelling either into or out of the light, so that they could be assigned to light or dark, respectively. Because $N = L + D$ in these calculations, the expanded formula is not comparable with that of Gunn and Cosway.

[4]All percentages rounded here and later.

TABLE II

The behaviour and activity of a single eighth-instar larva of *H. argentata* exposed in a dark-light chamber for six-minute periods at four different constant temperatures.

	Temperature, °C.			
	20.5	25.0	28.0	30.0
Photic orientation:	+	+	+	−
% time spent in lighted half:	72.2	47.2	25.3	7.5
Rate of travel, cm./min.				
(a) in light (L):	19.9	22.4	26.4	36.0
(b) in dark (D):	10.9	17.6	18.3	17.3
Turns/cm.				
(a) in L:	0.24	0.12	0.43	0.31
(b) in D:	0.55	0.58	0.55	0.52
Boundary reactions without crossing				
(a) L to D:	15	8	5	0
(b) D to L:	0	0	0	8
Boundary crossings without reaction				
(a) L to D:	2	3	6	2
(b) D to L:	2	2	5	1

night acclimatization so that it could be taken to temperatures above its ordinary distress range to illustrate travel rates, contact angles, and boundary reactions at an exceptionally high distress temperature.

Tables II and III show conclusively that the amount of time spent in the light is not a trustworthy indicator of an animal's response to light in an alternative chamber. Instead, at temperatures below reversal level, it is largely a function of the rate of travel in the confined space. Although rate of travel increases with increasing temperature in the lower part of the range both in the dark and the light, it increases much more dramatically in the light. The consistently slower rate in the dark results partly from the higher rate of turning there. In addition, some insects stop more frequently in dim than in bright light.

While the number of photopositive boundary reactions decrease with increasing speed of travel, the number of crossings into the dark that take place without any reaction increase. This is because the rapidly moving animal requires a larger contact angle with the boundary before it can detect it soon enough to react. As soon as it enters the dark, its speed decreases. Thus, it spends some time there before returning to the light. Consequently, as the temperature rises, the animal crosses the lighted area more and more rapidly, enters the dark more and more often, but does not move very rapidly therein at any temperature below distress levels. So it spends more of its time in the dark as the temperature rises, even though it is actually photopositive. Ignoring such consequences of an animal's orientation errors in an unnatural situation produces the misleading sort of index values shown in later tables, especially when the animal is very active.

TABLE III

The behaviour and activity of a single third-instar larva of *M. disstria* exposed in a dark-light chamber for six-minute periods at four different constant temperatures.

	Temperature, °C.			
	21.8	33.3	36.4	39.4
Photic orientation:	+	+	−	−
% time spent in lighted half:	84.2	41.1	16.9	11.4
Rate of travel, cm./min.				
(a) in L:	10.4	21.3	29.2	28.4
(b) in D:	6.4	7.3	8.4	12.7
Boundary reactions without crossing				
(a) L to D:	12	13	0	0
(b) D to L:	0	0	1	6
Maximum angle of contact (in degrees) with the boundary-line for boundary crossings without reaction				
(a) L to D:	16	56	90	90
(b) D to L:	90	90	52	70

I have shown elsewhere that not all individuals of a species are equally active (9, 10). When enough is known about a species to identify its sluggish individuals, the observer is at liberty to describe their photic reversal in any terms that appeal to him, because such individuals tend to stay in the light until the last possible moment (see, for example, figs. 36-41 in reference 9). Most investigators work unwittingly with mixtures of sluggish and active individuals, however, and the next examples show what may happen then.

Fifteen third-instar larvae of the arctiid, *Diacrisia virginica* (Fabr.), were selected at random from their feeding jars. They could be classified as nine active and six sluggish individuals. They were heated individually in the alternative chamber until they reversed their reaction to light, but they were held at each Centigrade degree for one minute to determine the percentage of time they spent in the light at each temperature. The results, together with the respective reversal temperatures, are shown in Table IV. (It is important to note that the percentages in the table do not show exactly when reversal occurred. The actual reversal temperatures listed were determined by changes in boundary reactions).

The larvae were then treated as a group in the chamber. Although their individual reversal points were noted, their positions also were recorded to provide data for calculation of their reaction indices. These records are shown in Table V.

Table IV shows that sluggish larvae tended to spend most of their time in the light until their reversal temperatures approached. Active larvae, however, continually left and re-entered the light long before they reached their reversal temperatures. According to the position records and index values in Table V,

TABLE IV

Percentage time spent in the lighted half of a dark-light chamber by active and sluggish third-instar larvae of *D. virginica* when the rising temperature was steadied for one minute at each one-degree interval.

	Temperature, °C.														Reversal temp.[a]
	31	32	33	34	35	36	37	38	39	40	41	42	43	44	
Active larva No.:															
1	68	100	75	0	0	73	50	0	0						37.2
2	88	75	60	35	53	58	53	0	25	0					37.9
3	0	65	0	95	56	28	75	76	0	0	0				39.0
4	100	100	100	100	78	45	100	55	38	0	0	10			39.5
5	78	100	100	100	100	58	63	21	41	0	0	0			39.5
6	100	65	100	96	38	41	55	75	50	48	0	0			40.2
7	100	23	61	33	75	91	43	83	70	40	0	0			40.5
8	100	100	100	0	0	5	100	0	0	100	5	28	0		40.9
9	0	60	100	65	70	65	100	58	25	41	100	0	61	0	43.0
															$\bar{x}$ 39.7
Sluggish larva No. :															
1	100	100	80	88	100	33	0	0							35.9
2	100	100	100	100	100	100	100	100	0	0					38.2
3	100	100	100	100	100	100	91	100	100	100	25	0			40.1
4	100	100	83	91	100	0	100	100	100	100	33	0	23	0	40.9
5	100	83	100	100	100	100	100	100	100	100	100	66	20	0	42.2
6	100	100	100	100	100	100	91	100	95	100	100	33	100	0	43.9
															$\bar{x}$ 40.2

[a] Determined by continuous observation of behaviour at the boundary-line.

TABLE V

High-temperature reversal of the photopositive reactions of fifteen third-instar larvae of *D. virginica* in a dark-light chamber as indicated by position records and indices of reaction-intensity, $\frac{100\ (L - D)}{N}$

Temperature, °C.	No. larvae in lighted half	Intensity of reaction (%)
31	14	+87
32	14	+87
33	14	+87
34	14	+87
35	13	+73
36	12	+60
37	12	+60
38	11	+47
39	10	+33
40	9	+20
41	9	+20
42	9	+20
43	7	− 7
44	4	−47
45	3	−60

TABLE VI

High-temperature reversal of the photopositive reactions of twelve eighth-instar larvae of *H. argentata* in a dark-light chamber as indicated by position records and indices of reaction-intensity, $\frac{100 (L - D)}{N}$.

Temperature, °C.	No. larvae in lighted half	Intensity of reaction (%)
19	10	+67
20	9	+50
21	7	+17
22	7	+17
23	8	+33
24	10	+67
25	6	0
26	5	−17
27	3	−50
28	5	−17
29	4	−33
30	5	−17
31	3	−50
32	1	−83
33	0	−100
34	1	−83
35	0	−100
36	0	−100

the group began to demonstrate photonegative behaviour between 42 and 43° C., but even by 45° C. the intensity of the reaction was not especially high. In reality, 12 of the 15 larvae had become photonegative by 40.9° C. (Table IV). Eight of the nine active larvae were negative by then, as were four of the six sluggish larvae. The tendency of the sluggish larvae to remain quiet in the light for long periods, however, when coupled with intermittent returns of active larvae to the lighted area after they had reversed their reaction, distorted the presentation considerably when only position records were considered. It is worth noting that the range of actual reversal temperatures for the whole group was 35.9 - 43.9° C., with a mean of 39.9° C. Therefore, the first beginning of reversal indicated by the changing sign of the index was some three degrees *above* the mean for the true reversal temperatures.

Since this error depends in part upon the activity level of the animals employed, it is not consistent, and one never knows from the index sign where the true reversal range may be. For example, the original group of 12 *H. argentata* larvae used earlier all moved about considerably when they were active. During one of their active periods, they were exposed in the alternative chamber and heated until they became photonegative, with the results shown in Table VI.

The position records and equivalent index values in Table VI suggest that transition from photopositive to photonegative behaviour began near 25° C., and that, for practical purposes, all larvae were photonegative by 32 - 33° C. But the distribution of the true reversal temperatures, as evidenced by boundary reactions, was:

T, °C.:	29.7	30.2	30.3	30.5	30.8	31.1	31.3	31.6	32.1	Total
No. larvae:	1	2	1	2	1	1	2	1	1	12

The temperature range within which true reversal took place was 29.7 - 32.1° C., with the mean at 30.8° C. Therefore, the transition temperature indicated by the index values is nearly five degrees below the *bottom* of the true reversal range. Evidently one cannot assume that true reversal lies consistently on one side of the range indicated by the index without knowing so much about one's material that employment of the index is hardly necessary. In fact, when the index is applied to light reactions, one cannot even be sure of obtaining accurate indication of the temperature above which a whole group is photonegative. And when results are so untrustworthy, they should not be used to interpret behaviour in natural situations.

It seems unwise, therefore, to continue to use methods whereby the positions of a number of animals are recorded intermittently without constant observation of their behaviour. Advocates of these "objective" methods would do well to inject into them rather more observation of individuals than they presently contain. This does not mean that I object to the use of groups in reversal experiments. I believe work with groups is essential if information on a range of reversal temperatures is to be sufficiently trustworthy for application in field studies. What I should like to see in such investigations is less consideration of the group as a collection of anonymous units and more emphasis on the behavioural changes of its constituent individuals. It is, after all, these behavioural changes which constitute reversal.

If an observer cannot keep separate the identities of individuals in large groups, then smaller groups must be used, and more group replications should be added to preserve the quantitative content of the data. No insurmountable problem of identification exists in most species when groups are held to some 15 animals. Even without artificial marking it is usually possible to select individuals that differ just enough in size, colour, or other noticeable characteristics to retain their identity in a mass of rapidly moving animals. Clipping a few bristles or marking with colours makes identification even easier.

Summary

The formula $\frac{100\ (L-D)}{N}$ should not be used to illustrate changes in photic response that occur when insects are heated in a dark-light alternative chamber. In fact, no method that depends primarily on intermittent records of the positions of the animals without continuous reference to their individual behaviour will provide a correct description of their changing response to light or the temperature range within which it occurs. This is because increases in their activity or speed of movement while they are confined in such a small space often carry the animals across the dark-light boundary before they can react to it. Since they move more slowly in the dark than in the light at any temperature, they may spend an increasing amount of time in the dark as temperature rises, even while they are still photopositive.

Truly photonegative behaviour is characterized by reactions on the dark side of the boundary that turn the insect back toward the dark. But these reactions cannot be seen for every individual unless observations are continuous. No correct account of photic reversal in groups can be obtained, therefore, without actual observation of this changed orientation as it occurs in each individual in turn. If individual responses are neglected, and the index of reaction intensity derived by applying the formula to position records is used instead, the indicated temperature for behavioural change within the group is always incorrect.

Furthermore, it may lie either up or down the temperature scale from the place where true reversal is concentrated, so that the observer never knows how to correct his calculation. Position records cannot be recommended, therefore, especially when laboratory results are destined for field application. Instead, calculations of group reversals should be based on collections of individual reversal temperatures accurately determined by direct observation. This can be done most easily by keeping groups small enough for rapid recognition of their constituent individuals and using an increased number of groups to preserve the quantitative content of results.

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The Unusual Pupal Mandibles in the Caddisfly Family Phryganeidae (Trichoptera)

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In most entomological textbooks and other general summaries the pupae of the order Trichoptera are characterized as having strong mandibles which are used to make a hole through the pupal enclosure, thereby permitting the escape of the pharate[1] adult. For the vast majority of caddisfly genera for which pupae are known this description is probably accurate enough, but it is somewhat less than accurate to describe the pupae of all caddisflies in this way.

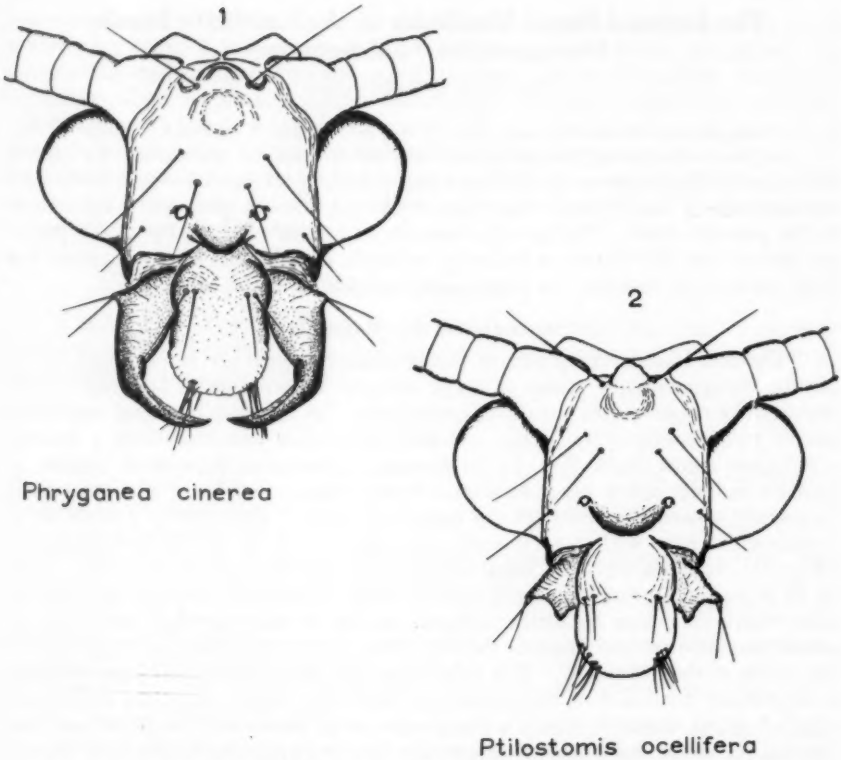
Structure of the Mandibles

The best known exceptions to this general statement are to be found in the family Phryganeidae, a group of about seventy known species confined to the northern portions of the northern hemisphere. In this family pupal mandibles are of two general types. One is a fully developed mandible with a heavily sclerotized apical blade (Fig. 1), in general, a functional appendage typical of pupal mandibles in the other families. Presumably mandibles of this type assist in making an exit hole through the pupal enclosure. The other is a short semi-membranous lobe with a very small sclerotized point on the ventral extremity (Fig. 2). It is unlikely that pupal mandibles of this type would be of any value at all in making an exit hole in the pupal enclosure because they are not heavily sclerotized, they have no well developed cutting or piercing edge, and they are much shorter than the labrum, thereby being prevented from working against the inside of the pupal case. It is quite clear that these pupal mandibles represent a degenerate condition of the sclerotized, knife-like type. It is this degenerate type of pupal mandible that is so very unusual in the order Trichoptera on the whole, yet about one dozen species in the family Phryganeidae are now known to have similar pupal mandibles, and when all phryganeid pupae become known, it is likely that this number will be increased to include something between a third and a half of all the species in the family.

The first evidence for the occurrence of degenerate pupal mandibles in the Phryganeidae came in 1903 with the description of the immature stages of the European species *Oligostomis reticulata* (L.), independently by Silfvenius, Struck and Ulmer, respectively. Additional examples were subsequently found in other European species: in *Hagenella clathrata* (Kolenati) by Struck (1904), and Silfvenius (1904); in *Holostomis atrata* (Gmelin) by Silfvenius (1904); and in *Holostomis phalaenoides* (L.) by Raciecka (1925). These observations were incorporated into general treatments of phryganeid pupae by Lestage (1921) and, most recently, by Hickin (1949). In North America degenerate pupal mandibles in the Phryganeidae were first recorded by Vorhies (1909) for *Ptilostomis ocellifera* (Walker). In 1921 Lloyd found similar pupal mandibles in *Oligostomis pardalis* (Walker)[2] and in *Oligostomis ocelligera* (Walker). Ross (1944) added *Banksiola crotchi* (Banks) to this list. Thus far, from my own studies of the immature stages of the Phryganeidae, three additional species, *Banksiola smithi* (Banks), *Banksiola dossuaria* (Say) and *Ptilostomis semifasciata* (Say) are now known to have degenerate pupal mandibles, too.

[1] A term used by Hinton (1946b) in reference to an instar which has become free from the cuticle of the preceding instar, although the old cuticle has yet to be ruptured and cast off.

[2] This species has been previously placed in the genus *Eubasilissa* Mart., following Martynov's classification of 1924. Martynov himself later retracted this view, stating in 1930 (p. 87) that on the basis of the male genitalia, *pardalis* could not be assigned to *Eubasilissa*, but that it could probably be included in the genus *Oligostomis* Kol. I have found a good deal of evidence from both adult and immature stages to support this view, and this will be presented in a forthcoming revision of the Phryganeidae.



Figs. 1, 2. Heads of pupae, face view; 1, *Phryganea cinerea;* 2, *Ptilostomis ocellifera.*

One very significant, although not unexpected, feature now becoming evident as the pupae of more phryganeid species become known, is that each of the genera, although created on grounds quite apart from the structure of these mandibles, has proved thus far to have consistently either degenerate or well-developed pupal mandibles.

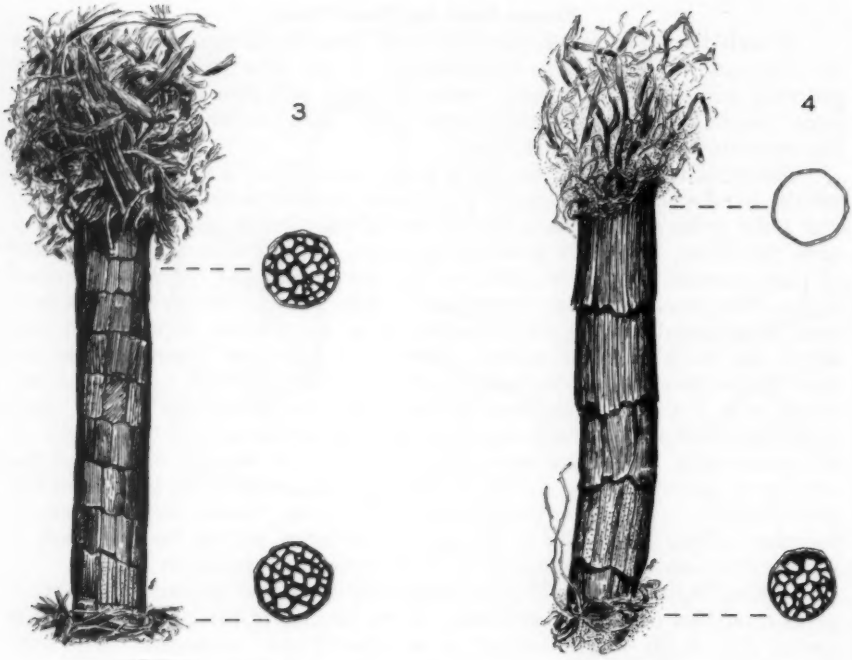
Hinton (1946a) has divided the endopterygote insect pupae into two groups: decticous pupae in which the mandibles are articulated and strongly sclerotized, and are capable of being moved by the muscles of the adult in such a way that escape from the pupal cell is gained; and adecticous pupae in which the mandibles are neither articulated nor capable of being moved by the muscles of the adult, and are of no use in providing a means of escape from the pupal cell. The pupae of the Trichoptera are classed as decticous, which is, of course, quite correct for the great majority of those species for which pupae are known. The degenerate mandibles in the Phryganeidae, however, can hardly be regarded as truly decticous because they bear no sclerotized cutting blade. On the other hand, there is some appearance of articulation in these mandibles (Fig. 2), and the apodemes of the pupal mandibles appear to be inserted in those of the pharate adult in the manner described by Hinton for typical decticous Trichoptera. Whether or not these degenerate phryganeid mandibles can actually be moved by the muscles of the adult, I do not know. These mandibles probably represent some intermediate structural condition between decticous and adecticous types.

Escape from the Pupal Case

If well-developed pupal mandibles with heavily sclerotized cutting edges are necessary to enable most caddisflies to escape from their pupal cases, as generally believed, then by what means do these phryganeids with degenerate pupal mandibles escape from their pupal cases? The answer to this is found in the structure of the cases themselves.

Examined from the outside, these pupal cases (Figs. 3, 4, 5) consist of the tubular larval case with a clump of plant pieces fastened around the anterior end, and a flat grille of fine silken strands woven into heavy meshes, known as a sieve membrane, across the posterior opening. Usually there are a few pieces of plant material fastened to this posterior sieve membrane. Taking a species such as *Phryganea cinerea* as representative of those with well-developed, sclerotized pupal mandibles (Fig. 1), examination of the interior of the pupal case shows that there is also an anterior silken sieve membrane fastened across the inside of the case a short distance behind its anterior lip (Fig. 3). The developing pupa is therefore enclosed within a chamber set off by a stout sieve membrane at each end, and presumably the well-developed pupal mandibles of this, and similar, species are used either to cut a hole through the side of the case, or to sever the silken meshes of this sieve membrane, thus permitting the pharate adult to escape from its enclosure. This is the classical interpretation of this phase of the life history of phryganeid caddisflies and has been assumed, it appears erroneously, by most workers to be typical for the whole family.

Taking *Ptilostomis ocellifera* as representative of the species with reduced pupal mandibles (Fig. 2), examination of the interior of the pupal case of this species (Fig. 4) shows no evidence of an anterior sieve membrane. The only closure at the anterior end of this pupal case consists of pieces of plant material fastened loosely together with silken strands. Although I have not seen the actual emergence from the case of forms with degenerate pupal mandibles, I have on several occasions observed that slight pressure on the case behind the pharate adult will cause it to move forward. It is a well-known fact that in the Trichoptera, movement, either forward or backward, within the pupal case is readily accomplished by means of the sclerotized hooks, some directed anteriorly, some posteriorly, on the dorsum of certain abdominal segments. These hooks are set firmly into the silken lining of the case, thereby permitting the insect to progress with considerable force from one point of firm anchorage to another. Pressure repeated progressively up the case behind the advancing insect eventually results in the insect's thrusting its head through the loose clump of plant pieces covering the anterior opening, apparently with no difficulty whatsoever. I assume that under natural conditions escape of the pharate adult from the pupal case is accomplished in much the same way at the appropriate time. It was only after I had become aware of this convenient arrangement in the pupae of several North American phryganeids that I discovered a similar observation had already been recorded by Vorhies as early as 1909 for *Ptilostomis ocellifera*, at that time misidentified as *Neuronia postica*: p. 660, "The pupal case is almost straight, closed at the anterior end by a loose mass of silk and vegetable debris, through which the pupa with its weak mandibles may make its way out." To the best of my knowledge, this observation of Vorhies has never before been cited or repeated. Thus far, I have been able to confirm it for six of the seven North American phryganeids listed previously as being definitely known to have reduced pupal mandibles. The one species known to have degenerate pupal mandibles for which Vorhies' observation has not been confirmed is *Oligostomis ocelligera*, which I have not yet reared.



Figs. 3, 4. Pupal cases, with cross-sections at the anterior and posterior ends. 3, *Phryganea cinerea;* 4, *Ptilostomis ocellifera.*

The evidence shows, then, that in the phryganeid species that I have studied in which the pupal mandibles have become degenerate, the habit of spinning an anterior sieve membrane has been lost. The closure over the anterior end of the pupal case is light enough to permit the pharate adult to push its way through to the outside without the assistance of sclerotized mandibles.

Phylogenetic Considerations

Reference has already been made to the rather obvious fact that these small, semi-membranous pupal mandibles in the Phryganeidae represent a degenerate condition derived from well-developed, sclerotized pupal mandibles in some ancestral form. Sclerotized, functional pupal mandibles are certainly a primitive character for the order Trichoptera, and all available evidence indicates that they are also a primitive character for the family Phryganeidae.

Logically, it would then follow that if these well-developed sclerotized pupal mandibles are essential to enable the pharate adult to escape from the case by cutting through the anterior sieve membrane, then the habit of spinning the anterior membrane would have been lost before the pupal mandibles degenerated to the point where they were useless in providing a means of escape. On the other hand, if well-developed, sclerotized pupal mandibles are not an essential part of the escape equipment of phryganeid pupae, then the degeneration of the pupal mandibles could have preceded, or more or less paralleled, the loss of the habit of spinning an anterior sieve membrane. Since the Trichoptera as a whole have

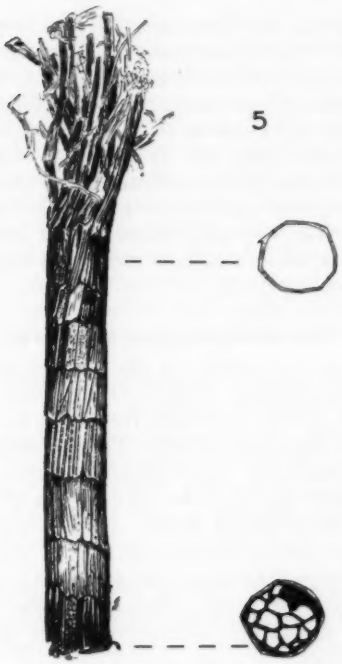


Fig. 5. Pupal case of *Banksiola crotchi*, with cross-sections at the anterior and posterior ends.

retained sclerotized pupal mandibles in one form or another, we can assume that they do serve some essential function, and this is very likely the escape from the pupal case. Thus, the former interpretation is probably correct, and in the Phryganeidae there is additional evidence for this. All pupae now known in the phryganeid genus *Agrypnia* have well-developed, sclerotized pupal mandibles, somewhat similar to those figured for *Phryganea cinerea* (Fig. 1). The pupal cases of at least two North American species, however, *Agrypnia vestita* (Walker) and *A. improba* (Hagen), in contrast to the pupae of *Phryganea*, have no anterior sieve membrane and are similar to the type in Fig. 5. Thus, there are species in which the habit of spinning an anterior sieve membrane has been lost, while the well-developed pupal mandibles have been retained. It seems likely, therefore, that during the evolution of phryganeid caddisflies the pupal mandibles degenerated after the habit of spinning a silken sieve membrane across the anterior end of the case had been lost, the mandibles no longer being essential in providing a means of exit from the pupal case. Whatever the function fulfilled by the anterior sieve membrane, we can only assume for the present that this was rendered unnecessary by some other development. This interpretation is based on the assumption that, in all species with degenerate pupal mandibles, the anterior sieve membrane is not constructed by the larva prior to the actual pupation. As indicated in the next section this assumption is not in accord with most of the published descriptions.

The method of constructing the larval cases in various phryganeid genera merits some comment here. The larval case in the genera with well-developed

pupal mandibles–*Phryganea, Agrypnia* and *Oligotricha*–is of a spiral type, that is, the case is formed of a single spiral band of plant pieces fastened side by side (Fig. 3). On the other hand, the larval case in most of the genera in which the pupal mandibles are reduced–*Ptilostomis, Hagenella, Oligostomis* and *Holostomis* –is composed of a series of complete rings of plant pieces joined end to end like lengths of stove pipe (Fig. 4). It might be supposed, then, that the degeneration of the pupal mandibles was in some way connected with this change in the structure of the larval, and hence the pupal, case, were it not for the existence of the North American genus *Banksiola.* In this genus the larval case is a typical spiral (Fig. 5), while the pupal mandibles are in the same degenerate condition as in *Ptilostomis* (Fig. 2).

The Anterior Sieve Membrane

For the North American species of the Phryganeidae that are known to have degenerate pupal mandibles, it has already been stated that whenever complete pupal cases have been available for examination, no evidence of the anterior sieve membrane has been found. This has been confirmed for six of the seven species now known to have degenerate pupal mandibles. The names of these have already been given in the first section of this paper. There are probably at least five more species which will also prove to have degenerate mandibles when their pupae are discovered, four of these because they belong to the genera *Ptilostomis* and *Banksiola,* in which all pupae known so far have degenerate pupal mandibles, and one other, *Hagenella canadensis,* because it is a member of the same genus as a European species which is known to have degenerate pupal mandibles.

The pupae of all the European species of the Phryganeidae are known, and these include four species that have degenerate pupal mandibles: *Oligostomis reticulata* (L.), *Hagenella clathrata* (Kol.), *Holostomis atrata* (Gmelin) and *Holostomis phalaenoides* (L.). References to descriptions of the pupae of these species have already been given in the first section of this paper. In these descriptions there is either no explicit reference to the anterior sieve membrane, or it is indicated that both ends of the pupal case are closed off with the sieve membranes which were believed to be characteristic of the Phryganeidae.

In view of the evidence already presented here, the anterior sieve membrane can hardly be regarded as characteristic of the Phryganeidae in North America. Furthermore, three of these four European species which have degenerate pupal mandibles are very closely related to North American species which also have degenerate pupal mandibles, but which are known not to spin an anterior sieve membrane. It seems to me, then, there is a possibility that the description of anterior sieve membranes in the pupal cases of species which have degenerate pupal mandibles may be in error. If these descriptions should prove to be accurate and the anterior sieve membrane really is formed, this would mean that there are species in which the pupal mandibles have become degenerate in spite of the fact that the habit of spinning an anterior sieve membrane has been retained. The immediate implication of this situation would be that well developed pupal mandibles are not as essential to break through the sieve membrane as has been assumed by most workers.

Pupae of none of the Asian species that would be expected to have degenerate mandibles have yet been described, as far as I am aware.

Another series of descriptions for which confirmation would be helpful concerns the holarctic phryganeid genus *Agrypnia.* Pupae have been described for about half of the seventeen or so species assigned to this genus, and all of

these have well-developed, sclerotized mandibles. As mentioned already in a previous section, examination of complete pupal cases of two North American species, *A. vestita* (Walk.) and *A. improba* (Hagen), has shown no evidence of an anterior sieve membrane. The front ends of the cases are closed with pieces of plant material drawn together with silken strands, much as in the genera with degenerate pupal mandibles. I have not seen complete pupal cases of any other species of *Agrypnia*. In one description, that of the northern Eurasian species *A. crassicornis* (McL.) by Silfvenius (1904), the comment is made that the anterior end of the pupal case is frequently open, and not closed with a sieve membrane. In the other descriptions of pupae of *Agrypnia* that I have seen, the anterior end of the case is described as being closed off with a sieve membrane in the same manner as the posterior end. Here again, discrepancies in descriptions of the anterior sieve membrane within a single genus suggest there is need for confirmation.

It is not, then, unreasonable to suggest that the pupal cases of the Phryganeidae could well be re-examined with these points in mind. It is scarcely necessary to add that subsequent descriptions of any phryganeid pupae would be all the more useful if details of the sieve membranes could be included. It is perhaps worth noting that there is here a rather unusual opportunity to enrich the fund of comparative systematic data on the Phryganeidae with a new set of observations from the behaviour of the immature stages.

Degenerate Pupal Mandibles in other Families of Trichoptera

There are, as far as I know, only two other recorded instances of degenerate pupal mandibles within the Trichoptera. Both of these occur in species of the hydropsychid subfamily Macronematinae: *Polymorphanisus bipunctatus* Brauer in the Belgian Congo and *Centromacronema auripenne* Rambur in Brazil. The pupae of both of these species represent the only knowledge yet available concerning the pupal structures in their respective genera.

A pupa from the Belgian Congo was briefly described and assigned to *Polymorphanisus* by Marlier (1943), and later identified as *P. bipunctatus* Brauer by Ulmer (1957). This pupa was without mandibles, but there is no information concerning the structure or closure of the pupal case.

An early record of a pupa from Brazil which lacked mandibles was given by Müller (1888) who assigned it to the genus *Macronema*. This record has been Thienemann (1905). Later, however, this pupa was reassigned to a species described by Müller, and published posthumously (1921), as *Macrostemum agnathum* Müller. After a close evaluation of Müller's work, Ulmer (1957) believes that this material should really be assigned to *Centromacronema auripenne* Brauer. It is stated that the pupal case was constructed of plant materials, and that both ends were closed with only some silken threads. Apparently, then, the degenerate pupal mandibles in this species are correlated with a reduction in the means of closure of the pupal case, as in the species of the Phryganeidae already described.

Summary

Although the pupae of the Trichoptera are usually characterized in textbooks and other general summaries as having sclerotized blade-like mandibles, this is not a completely accurate description for all groups. In the family Phryganeidae there are a number of species in which the pupal mandibles have become reduced to short semi-membranous lobes which lack a cutting edge. It is generally believed that well developed pupal mandibles are necessary to provide an escape hole through the pupal enclosure for the pharate adult by cutting

through the silken sieve membrane previously fastened across the anterior opening of the case by the larva. If this is true, then some alternate means of escape would be necessary in the species with degenerate pupal mandibles. This has apparently been accomplished through the loss of the larva's habit of constructing the silken sieve membrane across the anterior opening of the case, the case being closed off only with plant pieces drawn loosely together with silken strands. Aided by the dorsal abdominal hooks on the pupal integument, and not at all hindered by degenerate pupal mandibles, the pharate adult of these species is apparently able to ram its way through the loose covering to the outside at the appropriate time. The phylogenetic origin of these structures and habits is discussed.

Attention is drawn to the variations in the larval habit of spinning an anterior sieve membrane in this family, and it is suggested that if complete pupal cases of all species of the Phryganeidae could be examined specifically for the anterior sieve membrane, a set of useful systematic data on comparative behaviour of the immature stages would be gained.

Published records of degenerate pupal mandibles in two genera of another family, the Hydropsychidae, are summarized.

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A New Species of *Phyllophaga* from the Big Bend Region of Texas and Coahuila, with Notes on other Scarabaeidae of the Area

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During May, 1959, a number of uncommon species of Scarabaeidae were collected in or near the Big Bend National Park, Brewster Co., Texas. The object of this paper is to give distribution and habitat data on some of the rarer species and to describe one new species of *Phyllophaga*. Because much of the material is still unmounted, a complete list of species taken is not practical, nor can the exact number of specimens taken be given in some cases.

The Big Bend area of Texas and Coahuila is the type locality for a number of Scarabaeidae. Often the locality has been given as Big Bend National Park, Texas, or, if a local name has been included, such as "Juniper Spring", it is almost impossible to find on available maps. Because of the necessity of using obscure place names and because some of the roads are to be relocated, a map of the area is included, showing both the localities visited and type localities for some of the species discussed. Elevations in the park range from 1,800 feet at Boquillas Canyon to 7,835 feet in the Chisos Mountains. Vegetation varies from *Prosopis* and *Acacia* in the lowland desert areas to *Quercus*, *Juniperus* and *Pinus* in the mountains above 5,000 feet.

Several good general rains totalling two to three inches occurred during the month of May, normally one of the hottest and dryest months in the Big Bend area. These rains undoubtedly were an important factor in influencing the abundance and early appearance of some of the species mentioned.

Phyllophaga (*Listrochelus*) *arenicola* n. sp.

Holotype: Male. Length 9.5 mm.; greatest width 4.4 mm. Color brownish-yellow, pronotum slightly lighter than head or elytra. Head and pronotum shining; elytra dull, vaguely pruinose.

Clypeus (Fig. 7) with scattered coarse punctures; three times as wide as long; sides straight, converging anteriorly, becoming arcuate; with a shallow, anterior, emargination; margins evenly, moderately reflexed, except extreme posterior portions; central posterior portion slightly tumid; clypeal suture pronounced, impressed. Labrum rather deeply concave medially. Frons and vertex with numerous coarse punctures ending abruptly on the posterior half of vertex; vertex angled near anterior edge of impunctate area but lacking carina. Antenna ten-segmented, the three-segmented club approximately 1.4 times longer than the six preceding segments combined.

Pronotum seven-tenths as long as wide, widest at middle; posterior angles obtusely rounded; lateral margins with eight or nine erect setae on anterior

halves, not crenulate. Discal punctures of pronotum smaller and more widely spaced than those of head, the punctures rather evenly scattered, separated from each other by distances of from two to five diameters.

Scutellum with color and punctures similar to those of pronotum. Elytra more closely punctate than pronotum; each puncture with a minute tan seta; discal costae absent; elytra with scattered, short, erect, tan setae along margins. Pygidium only moderately convex; surface finely punctate, each puncture bearing a minute tan seta; surface between punctures finely alutaceous.

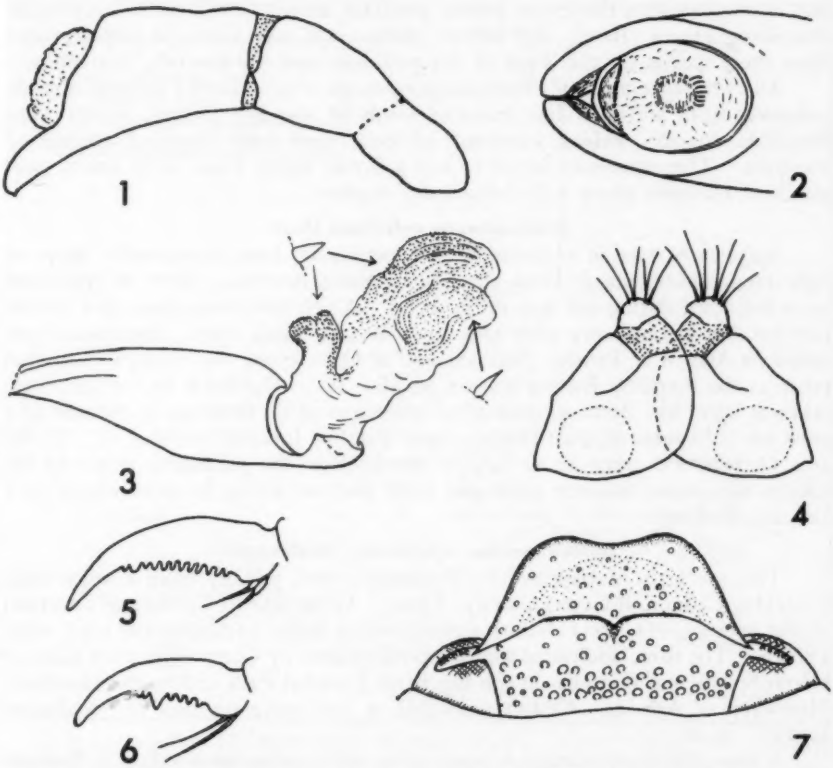
Abdomen evenly rounded medially; terminal segment unmodified; punctures present only laterally and in a transverse line near the posterior margin of each sternite; each puncture with a minute tan seta, the setae larger on the terminal segment; last sternite approximately one-half as long as penultimate sternite. Metasternum slightly more heavily punctate than pronotum, each puncture with a fine tan seta. Fore tibia tridentate, the upper tooth noticeably closer to base than to apex. Each tarsal segment with a distinct carina extending the length of the lower margin, which is not produced apically; each tarsal claw (Fig. 5) pectinate below in a single line and lacking longer teeth; number of distinct pectinations varying from 10 to 15; several pectinations often closely joined. Posterior tibial spurs jointed (movable), moderately slender; longer spur approximately as long as basal posterior tarsal segment measured from apex to basal constrictions; both spurs very thin and semi-transparent in outer thirds and along lateral edges. Hind tibia with a faint longitudinal carina along dorso-mesal edge, most evident in basal half; tibial apices with 17 and 19 setae or spinules.

Genitalia (Figs. 1 and 2) symmetrical; parameres blunt at apices, touching, excavated beneath along inner half; aedeagus (Fig. 3) with anterior, scoop-shaped, sclerotized plate, the latter becoming cylindrical posteriorly; scattered patches of minute teeth present in internal sac.

Allotype: Female. Length 10 mm., greatest width 4.7 mm. Essentially similar to holotype except in following respects: antennal club approximately as long as six preceding segments; pygidium not as elongate, slightly less convex; abdomen more tumid, segments 2 to 5 appearing connate medially, apex of last sternite with very slight median indentation; tarsal claws (Fig. 6) each with a short median tooth, margin behind the tooth distinctly pectinate; tibial apices with 21 and 22 setae or spinules; longitudinal dorso-mesal carina of tibia obsolete; genitalia as in Fig. 4.

Holotype: male, Boquillas, Coahuila, Mexico, May 23, 1959, H. Howden and E. Becker, at light. (C.N.C. No. 7079). Allotype: female, same data as type (CNC). Paratypes, seven males and three females with following data: two males same data as type; four males, one female, Boquillas Canyon, Big Bend National Park, Texas, May 25, 1959, H. Howden and E. Becker, at light; one male, two females, three miles west of Castolon, Big Bend National Park, Texas, May 14, 1959, H. Howden and E. Becker, at light. Paratypes are deposited in the Canadian National Collection, Illinois Natural History Survey, United States National Museum, and in the personal collection of Mr. L. J. Bottimer, Kerrville, Texas.

Variation in the paratypes is moderate; length ranges from 9 to 11.5 mm. and greatest width from 4.1 to 5.1 mm. Color varies from tan to brown, the specimens from Boquillas, Mexico, being lightest in color, the ones from Boquillas Canyon, Texas, the darkest. The three specimens from three miles west of Castolon have shining elytra, and lack any trace of the pruinosity evident on the elytra of all of the other specimens. The lack of pruinosity is perhaps due to abrasion, since the clypeus and fore tibia of the three specimens appear



Figs. 1-7. *Phyllophaga* (*Listrochelus*) *arenicola* n. sp. 1, male genitalia, right lateral view; 2, male genitalia, dorsal view; 3, aedeagus and everted endophallus of male genitalia; 4, female genitalia; 5, male, left front tarsal claw; 6, female, left front tarsal claw; 7, head of holotype.

worn. Noticeable variation occurs in the clypeus, which may have the sides nearly straight or broadly arcuate, which may be noticeably reflexed anteriorly or only slightly so, and which may have the disc nearly flat instead of tumid. One male from Boquillas Canyon, Texas, has nine- instead of 10-segmented antennae, the fourth and fifth segments seemingly fused. Number and size of dorsal punctures are fairly constant, as is the shape of the pygidium. Apical spinules on the hind tibiae vary from 17 to 20 in the males and from 21 to 22 in the females. The male genitalia appear essentially similar, showing only a slight difference in the length of the parameres. One female has a small, oval, median. hump on the penultimate sternite, with eight setae scattered along the posterior edge of the hump.

Phyllophaga arenicola does not appear to be closely related to any other described species in the subgenus *Listrochelus*. The vertex lacks a definite carina, the punctures of the head are scattered (Fig. 7), antennae usually 10-segmented, claws pectinate along one margin (Figs. 5 and 6), pygidium and abdomen unmodified, and male genitalia symmetrical (Figs. 1, 2, and 3). The species does not readily key out to any *Listrochelus* in Saylor's key (1940, p. 63),

but, if one considers the vertex poorly punctate, *arenicola* will fall in the couplet containing *cavata* (Bates) and *micros* (Bates). It may easily be differentiated from these species by the shape of the pygidium and the genitalic characters.

All of the specimens of *Phyllophaga arenicola* were collected at light in sandy mesquite areas within a few hundred yards of the Rio Grande River. The Boquillas, Mexico, habitat consisted of loose sand with scattered clumps of mesquite. The other two localities had a firmer sandy loam, with nearly pure stands of mesquite along well-defined dry washes.

***Onthophagus velutinus* Horn**

Apparently rare in collections, this species has been occasionally taken at light from southwestern Texas through southern Arizona. Over 30 specimens were collected during our stay in Big Bend. A few specimens came to Coleman lanterns, but the majority were taken at a 40-watt black light. Specimens were taken on May 8 at Panther Junction and at Oak Spring and a single male was taken at the Boquillas Ranger Station on May 28. In addition to the specimens taken at light, Mr. Bottimer took three specimens of *O. velutinus* in the nest of a pack rat (*Neotoma albigula* Hartley) near Panther Junction on May 12. In this area *O. velutinus* seems to be largely restricted to the peripheral slopes of the Chisos Mountains between 4,000 and 5,000 feet, occurring in areas where pack rats are abundant.

***Bolborhombus angulatus* (Robinson)**

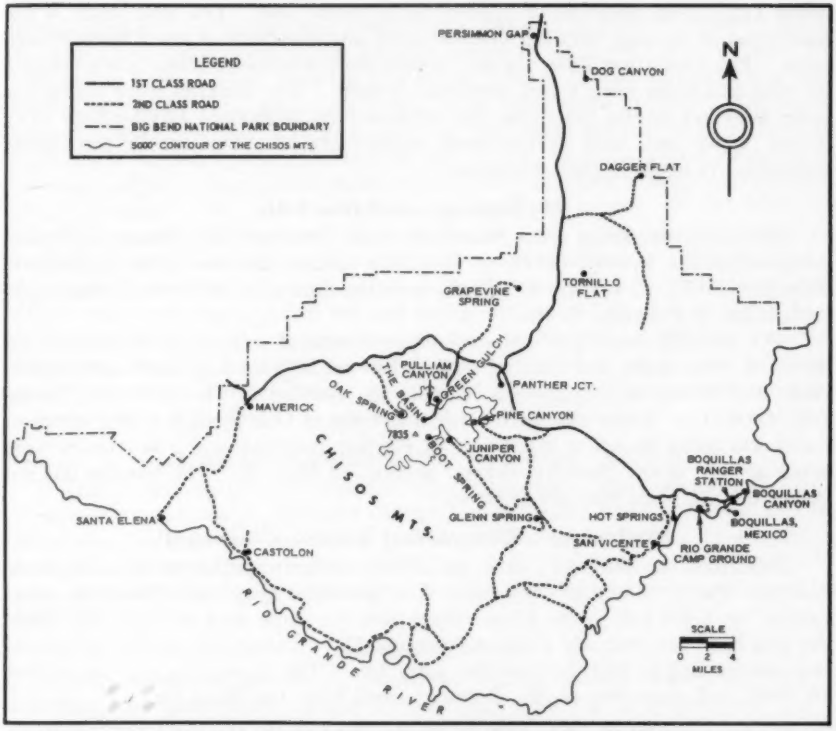
This species was described by Robinson (1947, p. 170) from a single male from Dog Canyon, Brewster County, Texas. At the time of Cartwright's revision of the genus (1953, pp. 117-120) a total of four males, including the type, were known. The three additional specimens mentioned by Cartwright were taken at Glenn Spring and Boquillas in the Big Bend National Park and in the Huachuca Mountains of Arizona. Cartwright (1953, p. 118) gave the time of occurrence as July 7 to 29.

A few additional specimens, both males and females, were taken at Tornillo Flats and at Panther Junction (Park Headquarters) in the Big Bend National Park from May 12 to May 28, 1959. The Tornillo Flats specimens came to Coleman lanterns placed in a dry wash, while the specimens taken at Panther Junction came to a 40-watt black light. In most cases the specimens were found at the edge of the lighted area.

Morphologically, *B. angulatus* is one of the few species in the tribe Bolboceratini in which the characters of the head are nearly identical in the sexes. In the females, length varied from 9.4 to 13.1 mm. and greatest width from 5.7 to 7.7 mm. The carina of the anterior edge of the clypeus is slightly more pronounced in the females, while the median and posterior carinae are slightly smaller than in the males. Punctures of the head and pronotum seem more pronounced in the females than in the males, but differences seem due to normal variation, regardless of sex.

***Trox carinatus* Loomis**

A total of 14 specimens of this species have been recorded (Vaurie 1955, p. 63; 1959, p. 45) from southern Arizona, southern New Mexico, and southwestern Texas in the United States and from Chihuahua in Mexico. Eight specimens were taken between May 12 and May 23 at the following localities in the Park: Panther Junction (Park Headquarters), Boquillas Ranger Station, and Oak Spring. Most of the specimens came to a 40-watt black light, but several specimens were taken at Oak Spring on chicken feather bait by L. J. Bottimer. A single specimen was collected at the black light on May 31 at Ft. Davis, Texas.



Map of Big Bend National Park, Brewster County, Texas, showing the collecting localities. The 5,000 foot contour of the Chisos Mountains is shown for reference.

***Benedictia pilosa* Sanderson**

This unusual monotypic genus was described by Sanderson (1939, pp. 1-4) from Presidio, Texas, and the Big Bend National Park. Two males of this species were taken at Coleman lanterns two miles west of Castolon on May 21. The locality was in a pure stand of mesquite near a large sandy dry wash, approximately a quarter of a mile from the Rio Grande River. I have seen additional specimens labeled Big Bend National Park, Texas, May 24, 1950, and Coahuila, Mexico, Sierra de Tlahualilo, 4,000 ft., Ojo de Agua nr. Durango line, July 18, 1952, C. C. Kersting.

***Serica porcula* Casey**

This is a common western species, but only a single specimen has been reported from Texas (Dawson, 1947, p. 232). Occasional specimens were taken above 5,000 feet in the Chisos Basin at light and on gray oak (*Quercus grisea* Liebm.). The first specimen was collected April 28 in the Basin, others were taken at scattered dates throughout May.

***Phyllophaga idonea* Sanderson**

The type series of 14 specimens was collected in the Chisos Mountains in Juniper Canyon and at Upper Juniper Spring at an elevation of 5,000 feet. According to Sanderson (1948, p. 4), the beetles were taken in the oak-pine-juniper habitat that occurs widely in the Chisos Mountains above 5,000 feet. Two specimens of *P. idonea* were taken at light on May 18 several hundred yards up Lost

Mine Trail at an elevation of approximately 6,000 feet. The trail starts at the main road at the pass between Green Gulch and the Basin in the Chisos Mountains. The vegetation along the trail where the beetles were taken was a mixture of oaks and pines with a few scattered juniper. The lanterns were set in the same place on several occasions, but attracted no additional *Phyllophaga* since strong winds and cool temperatures made light trapping for beetles rather unproductive at the higher elevations.

***Phyllophaga pusillidens* Fall**

Originally described from four males from Brewster Co., Texas, as *Phyllophaga microdon* by Fall (1929, p. 113), this species has been seldom collected. Reinhard (1950, p. 41) knew of only two specimens in addition to the types, both taken at Presidio, Texas.

We found *P. pusillidens* not uncommon in several areas in the Park. A long series of both males and females were taken feeding on *Lepidium lasiocarpum* Nutt. and *Mentzelia oligosperma* Nutt. in the evening of May 8 at Oak Spring (alt. 4,000 ft.). Some males were taken at light at Oak Spring; a long series of males was taken May 8 at black light at Panther Junction; and a few males were taken at light at the Boquillas Ranger Station on May 28. The females did not come to light, since they are flightless.

***Phyllophaga* (*Listrochelus*) *bottimeri* Reinhard**

Described by Reinhard (1950, pp. 29-30) from six specimens from Big Bend National Park. A single dead male was found on gray oak (*Quercus grisea* Liebm.) at 5,400 feet in the Chisos Basin near the cabin area on May 29. Since the area had been intensely collected through May, it seems likely that the species was just starting to emerge when the party left. The type series was taken June 10, 1948, and according to Mr. Bottimer came from the Basin area.

***Phyllophaga* (*Listrochelus*) *planeta* Reinhard**

This species was described by Reinhard (1950, pp. 30-31) from a single pair collected at Ft. Davis, Texas. Reinhard compared his species to *meadei* Saylor, stating that it differed in the shape of the male genitalia and female pygidium. A series of 19 specimens, seemingly referable to *P. planeta*, were collected at night by beating Mexican pinyon pine (*Pinus cembroides* Zucc.) in Green Gulch at altitudes ranging from 5,000 to 5,500 feet. While the females in the series are easily referable to *P. planeta*, lacking the transversely gibbose pygidium of *P. meadei*, the genitalia of the males seems intermediate between the two species.

***Plusiotis gloriosa* LeConte**

This handsome scarab occurs on juniper from western Texas to Arizona. Occasional specimens were taken at black light in the Basin area at 5,400 feet from May 18 throughout the rest of the month. I have seen specimens from the Chisos Mountains and Alpine, Texas, taken in July, but the May records seem unusually early.

***Chlorixantha chapini* Cartwright**

This brightly colored cetonid was described by Cartwright (1939, pp. 363-364) from four specimens taken in June in the Big Bend National Park. It has been rarely taken since. We found *C. chapini* widely distributed in the lower elevations of the Chisos Mountains between 4,000 and 6,400 feet. Specimens were first taken flying around the yellow blossoms of a broad-leafed *Opuntia*. However, only a few specimens were taken in this fashion. The host of *C. chapini* was discovered purely by chance. Members of the collecting party

were collecting the buprestids, *Thrincopyge alacris* Lec. and *T. ambiens* (Lec.) in sotol (*Dasylirion leiophyllum* Engelm.) when a specimen of *C. chapini* was seen at the base of a leaf near the top of the plant. Additional specimens were soon discovered. The specimens, while easily seen, were extremely difficult to collect. Sotol is similar in form to some of the yuccas, growing four to five feet high, with the stiff leaves occurring at the top of the plant. The leaves themselves are edged with recurved spines, making even careful investigation extremely uncomfortable! The best method of capturing the beetles was to have one person, wearing heavy gloves, bend the leaves apart while another person extracted the specimen with a pair of 12-inch forceps. Most of the specimens of *C. chapini* were taken in large plants with flower stalks. Some recently dead plants were torn apart, and in the soft center several old pupal cells, possibly of *C. chapini*, were found. Specimens were taken in Big Bend from May 4 to May 28 at the following localities: Panther Junction, Pine Canyon, Green Gulch and at 6,400 feet near Panther Pass at the head of Green Gulch. A single specimen was also taken at Ft. Davis, Texas, May 30 in a large sotol.

***Aphonides* (*Anoplognatho*) *dunnianus* (Rivers)**

This is an uncommon dynastid which has been taken occasionally from western Texas through southern Arizona. Specimens were taken in the Big Bend area only in the vicinity of the Boquillas Ranger Station in a stand of mesquite. Five specimens came to a 40-watt black light between May 23 and 28. One specimen was found crawling in a small dry wash shortly after dark on May 28.

Acknowledgments

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Summary

A new species, *Phyllophaga* (*Listrochelus*)*arenicola*, is described from Boquillas, Mexico, and neighboring localities in the Big Bend National Park, Brewster County, Texas. Notes on collecting in the Big Bend area and habitat data are given for *Onthophagus velutinus* Horn, *Bolborhombus angulatus* (Robinson), *Trox carinatus* Loomis, *Benedictia pilosa* Sanderson, *Serica porcula* Casey, *Phyllophaga idonea* Sanderson, *Phyllophaga pusillidens* Fall, *Phyllophaga bottimeri* Reinhard, *Phyllophaga planeta* Reinhard, *Plusiotis gloriosa* LeConte, *Chlorixantha chapini* Cartwright, and *Aphonides dunnianus* (Rivers). A map of the localities visited in the Big Bend National Park is included.

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Field Tests of Some Hydrolyzed Proteins as Lures for the Apple Maggot, *Rhagoletis pomonella* (Walsh)[1]

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During the past decade the attractiveness of various hydrolyzed proteins to several species of tephritid flies has been established and these materials have been used in poison bait sprays, in fly traps, and in studies on dispersal habits. Several workers have reported more satisfactory control when enzymatic yeast hydrolysates or acid hydrolysates of corn protein were added to malathion sprays: Steiner (1952, 1955a, and 1955b) for the Mediterranean fruit fly (*Ceratitis capitata* Wied.), the oriental fruit fly (*Dacus dorsalis* Hendel), and the melon fly (*Dacus cucurbitae* Coq.); Shaw (1955) for the Mexican fruit fly (*Anastrepha ludens* Loew); Orphanidis *et al.* (1958) for *Dacus* adults on olives; and Marucci (1958) for the blueberry maggot (*Rhagoletis pomonella* (Walsh). Orphanidis *et al.* have also reported that the addition of casein hydrolysate or the acid hydrolysates of corn protein to the recommended lure of ammonium sulphate increased the captures of *Dacus* as much as twelve times. Although most of the work with these attractants has concerned control, Barnes (1959) has used them to advantage in biological studies. He labelled natural populations of the walnut husk fly, *Rhagoletis completa* Cress., with a radioactive tracer by attracting the flies to feeding stations of Staley's insecticide bait No. 7 (acid hydrolysate of corn protein) plus the isotope P^{32}. By subsequent trapping he determined the field movements of the adults in and out of walnut orchards.

Although hydrolyzed proteins, especially enzymatic yeast and acid hydrolysates of corn protein, have been shown to be attractive to some species of fruit flies, many species have not been tested concerning these and other protein hydrolysates. This is a report on the attractiveness of four enzymatic hydrolysates (soy, yeast, casein, and lactalbumin)[2] and two acid hydrolysates of corn protein (Staley's insecticide baits Nos. 2 and 7)[3] to the apple maggot, *Rhagoletis pomonella*. Additional notes are given on the use of traps for timing control sprays.

[1]Contribution No. 19, Research Station, Canada Department of Agriculture, Fredericton, New Brunswick.
[2]Manufactured by Nutritional Biochemicals Corporation, Cleveland, Ohio.
[3]Manufactured by A. E. Staley Manufacturing Co., Decatur, Illinois.

TABLE I

Total numbers of *R. pomonella* taken in traps with various lures in apple trees, 1957 to 1959

Lure	1957	1958	1959
Soy hydrolysate	81	130	35
Casein hydrolysate	65	125	26
Lactalbumin hydrolysate	52	67	26
Yeast hydrolysate	34	86	21
Urea	32	—	—
Water	3	—	—
Staley's No. 2	—	78	17
Staley's No. 7	—	81	17

Procedure

Aequous solutions of the materials were tested in traps placed in a commercial orchard. In 1957 the four enzymatic hydrolysates were compared with a recommended lure of urea-sodium hydroxide (Hodson, 1948) and a water control. In 1958 and 1959 they were compared with the acid hydrolysates of corn protein.

The traps were domestic baking pans (three inches deep and eight inches in diameter) which were hung four to eight feet above ground in the apple trees. Six traps, one for each lure, were hung in each tree. In 1957 there were 48 traps for eight replications of each lure, and in 1958 and 1959 there were 72 traps for 12 replications of each lure. The lures were assigned to the pans so that each lure occurred equally often in all quadrants of the trees. Half a liter of lure was placed in each trap and renewed at weekly intervals from July 1 to September 30.

The concentration of the recommended lure was two per cent urea and three per cent sodium hydroxide, which Hodson (1948) claims is a more effective lure of *R. pomonella* than ammonium carbonate or ammonium acetate. The hydrolysates were tested as one per cent solutions. One gram of sodium hydroxide was added to each 100 cc. of hydrolysate solution to prevent putrefaction, which aside from its obnoxious odours, makes the solutions cloudy and also attracts large numbers of various dipterous species. The last two effects necessitate straining of the solution and sorting of the flies to determine the catch of *R. pomonella* and considerably lengthen the time required to record the catch. The sodium hydroxide prevents putrefaction possibly in the same manner as that attributed by Gow (1954) to antibiotics. A few drops of Triton B 1956 were added to all solutions to lower the surface tension, as Hodson (143) claims that this ensures a more rapid immersion of flies and thereby reduces the chance of escape.

The numbers of trapped flies were recorded daily, whenever possible, and the females preserved in 70 per cent alcohol for future examination to determine the percentage containing mature eggs.

Emergence of adults from the soil was recorded daily from cages 'salted' with infested apples taken from the trees containing the traps.

Results and Discussion

In general, the enzymatic hydrolysates were more attractive than the recommended lure or the acid hydrolysates ((Table I). In 1958 soy and casein hydrolysates were appreciably more attractive than the acid hydrolysates. In 1959 all the enzymatic hydrolysates were more attractive than the acid hydrolysates.

TABLE II

Records on emergence and trapping of *R. pomonella*, 1957 to 1959

	1957	1958	1959
Number captured	267	567	142
Percentage females	57.0	64.0	60.0
Number emerged in cages	—	219	377
Percentage females	—	52.0	56.0
Period of capture	July 16 - Sept. 5	July 17 - Sept. 10	July 13 - Sept. 8
Period of emergence	—	July 12 - Aug. 25	July 6 - Sept. 15
Peak of capture	August 12	August 13	August 5
Peak of emergence	—	July 30	July 22

Soy hydrolysate trapped the greatest number of flies in each year. In tests with the oriental fruit fly, Gow (1954) also found that soy was a better attractant than the other enzymatic hydrolysates. Enzymatic yeast and Staley's insecticide baits Nos. 2 and 7 differed little in attractiveness; this agrees with the report of Lockmillar and Thomas (1957). Although these three materials were less attractive than soy or casein, they may be useful in poison bait sprays as Steiner (1955b) found that the most efficient lures in traps may not be the best in sprays. Enzymatic casein was second in attractiveness only to soy.

More females than males were captured in each year (Table II). Apparently the materials were about equally attractive to the two sexes, however, as more females than males emerged in the emergence cages.

Evidently many of the flies had emerged about a week before they were captured in the traps, as indicated by emergence and trapping records (Table II), and also by the presence of mature eggs in the ovaries of trapped females. Dean (1935, p. 17) reported that the eggs usually require nine to ten days to develop after the adult emerges. Over 50 per cent of the trapped females contained some mature eggs, indicating that they were at least nine days old. Therefore, as there was an appreciable difference between the time of emergence and the time of capture, traps are not as reliable as emergence cages for timing control sprays. Hodson (1943) considers traps with ammonia lures as reliable as emergence cages because most of the flies trapped were less than 15 hours old.

Summary

Four enzymatic protein hydrolysates were each more effective lures for adults of the apple maggot than a previously recommended lure of urea-sodium hydroxide. Enzymatic soy and casein hydrolysates were more effective lures than two acid hydrolysates of corn protein (Staley's insecticide baits Nos. 2 and 7). Soy hydrolysate was the most attractive of the enzymatic hydrolysates. The materials were about equally attractive to the two sexes. Flies were not captured in traps until about a week after they emerged, so that trapping records are unreliable for the timing of control sprays.

Acknowledgments

The author gratefully acknowledges the helpful criticism of Dr. R. H. E. Bradley, Head of the Entomology and Plant Pathology Section, and of Dr. M. E. MacGillivray, Dr. J. A. McAllan, and Dr. R. Bagnall of the same section, in preparing the manuscript.

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A Note on Sexual Dimorphism in *Sitophilus*[1] Weevils

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The advantages of being able to determine the sex of insects by means of external characters are obvious, particularly when, as with the *Sitophilus* weevils, they have been favoured as experimental material by many workers. In *Sitophilus oryza* (L.), the sex can apparently readily be determined by reference to the relative length of and type of puncturing of the rostrum (Richards, 1947). There has seemed, however, to have been some doubt about a similar reliable method of determining sex in *Sitophilus granarius* (L.). Richards (1947) stated that there was no certain way of determining the sex of this species without risking injury to the female. In a later paper (1948) he implied, in a footnote, that a specimen could be sexed by reference to the length and slenderness of the rostrum. This had been given as a method of sexing these insects by Back and Cotton (1926).

In a series of recent observations, in which many scores of weevils were examined externally and later checked by dissection, we have found another means of sexing *S. granarius*. We have also found that this method and the rostrum method are valid for only one of the two strains of weevils available to us, namely the GG strain (Musgrave and Miller, 1958).

In the GG strain males have a slight, roughly triangular depression on the ventral surface of the abdomen, postero-medially to the last pair of coxae,

[1] *Sitophilus granarius* and *S. oryza* are used here for the granary and rice weevil respectively, in accordance with common North American usage, instead of *Calandra granaria* and *C. oryzae* as employed by many authors elsewhere. A complex situation is analysed by Back and Cotton (1926) and Vaurie (1951).

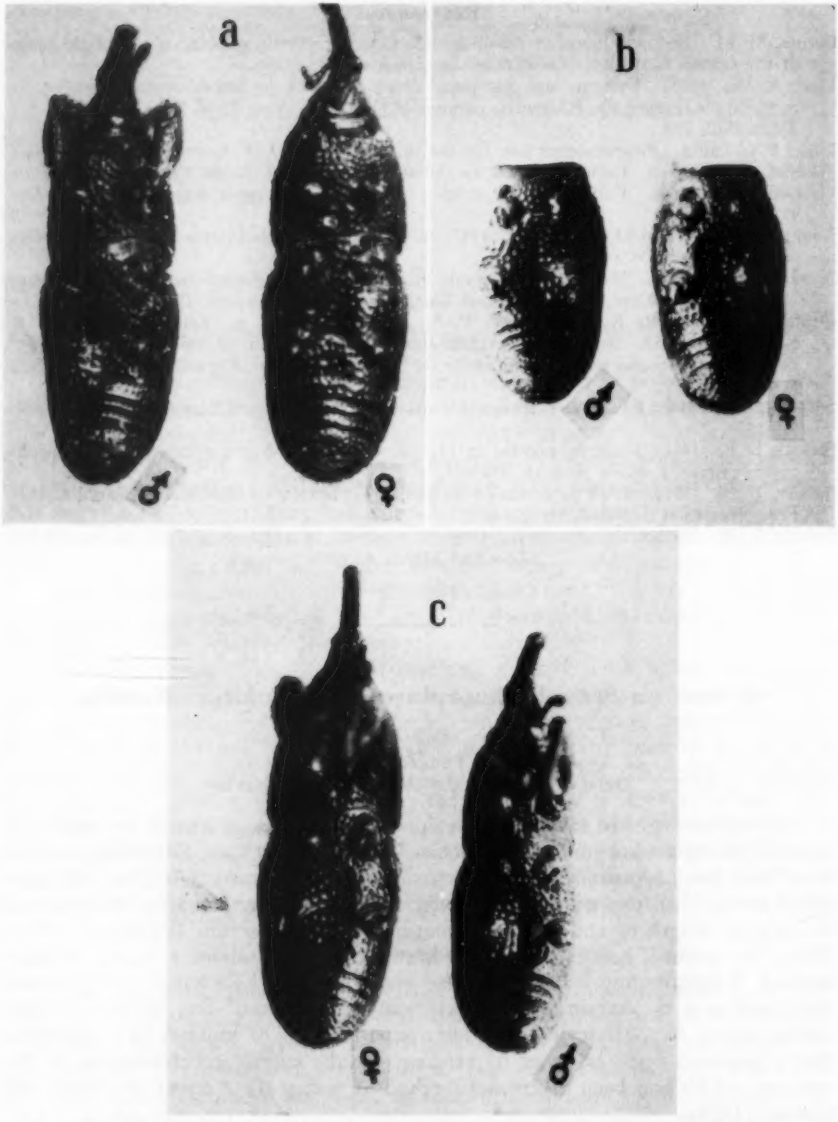

Fig. 1. Photographs of ventral views of weevils, *Sitophilus granarius* (GG strain), to show triangular depression in the middle line posterior to hind coxae in males. In all specimens, mid and hind legs have been removed distal to coxae; in some specimens, forelegs have also been removed. The letters *a*, *b*, *c* are assigned to photographs of different pairs of weevils.

whereas the similar area of the female abdomen is flat or slightly raised (Fig. 1). It has not been possible to determine the sex of members of our other strain (MW) with the same reliability by these or other external methods.

This interesting state of affairs may explain why some investigators have had mode difficulty than others in sexing *S. granarius*, for the weevil seems to occur in many strains. Here, too, is yet another difference between the microbiologically different strains GG and MW.

We take this opportunity to thank Dr. W. E. Heming, Head, Department of Entomology and Zoology, in whose department this work was performed, and Dr. M. V. Smith, Department of Apiculture, for help with photography.

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Cocooning Behaviour of Overwintering Codling Moth Larvae[1]

By C. R. MacLellan

Codling moth larvae seeking overwintering sites usually spin up during hours of darkness on the trunks and larger branches of apple trees rather than in the soil or in debris under the trees. The number on the ground depends on the suitability for cocooning sites of the bark on the tree and on the amount and type of debris on the ground. Gould and Geissler (1941) found that larvae did not spin up in bare and compact soil and Steiner (1929) observed that most larvae returned to the tree to spin cocoons when there was little or no litter beneath the trees. Baker (1944) reported eight to nine per cent spun up on the ground beneath unscraped trees, and 18 per cent where the loose bark scales were removed. Others (Headlee (1929), Worthley (1932), Gnadinger *et al.* (1940), Woodside (1941), and Stultz (1946)) found that under natural conditions from 0 to 14 per cent spun up in the soil, in the cover crop, or in the debris on the ground.

Spring counts of overwintering codling moth larvae on apple at Kentville indicated that a high percentage selected trunk sites and that there was heavy winter mortality of larvae choosing other cocooning sites. The study reported upon here was undertaken to gain further knowledge of cocooning behaviour of codling moth larvae.

Methods and Results

The larvae used in the tests were collected in the fourth or fifth instar in the field. The larvae used for the cocooning experiment were immature and were made radioactive by allowing them to feed for 48 hours or more on cubes of apple dipped briefly in a 50 μc/ml. solution of radiophosphorus. For the movement experiment the larvae were kept in storage until just mature and made radio-

[1]Contribution No. 1031, Research Station, Canada Department of Agriculture, Kentville, Nova Scotia.

TABLE I

Location of radioactive codling moth larvae or their cocoons two weeks after their release on the fruit of three trees as follows: Tree 1, on the upper third; Tree 2, on the lower third; Tree 3, on the ground under the tree.

Number of Live larvae,			Larvae or cocoons on:			Total recovered
Tree number	larvae released	remnants or cocoons on ground	Main trunk	Lower branches	Upper branches	
1	37	5	13	5	4	27
2	37	0	14	3	3	20
3	43	8	15	0	0	23
Totals	117	13	42	8	7	70

active by simply placing them in the solution for three to five minutes. Radioactive larvae were easily detected with a portable particle counter at an unobstructed distance of eight inches.

Cocooning Experiment — 1958

The first experiment was conducted in September, 1958, in an isolated orchard. Treated larvae were released as follows: 37 larvae each on fruit on the upper one-third portion of tree number 1 and lower one-third portion of tree number 2; and 43 larvae (six of which were unthrifty) on fruit resting on the ground beneath tree number 3. To aid penetration by the larvae, the skin of the fruit was nicked with a pen knife and observations showed that many larvae used the nicks as points of entry. Two weeks later the debris on the ground beneath all three trees was carefully gathered and searched for the released specimens. The cleared ground and the trees also were carefully scanned with the particle counter.

Table I summarizes the results of the cocooning experiment. Sixty per cent of the 117 larvae released were located, 73 per cent of those released on tree number 1 were recovered and 54 per cent from each of trees numbers 2 and 3. Of the six live larvae found on the ground three were still within fruit under tree number 3, one was spun up in a mummified fruit, and two were spun up in small bark scales. There was one dead partially spun up larva in the crown of a strawberry plant and remnants of three larvae were found near the points of release of the six unthrifty larvae. Three torn radioactive cocoons were found on the ground.

Of the larvae released, 57 prepared cocoons on the trees, but 35 larvae were removed by woodpeckers. Forty-two cocoons were found on the main trunks, eight on the lower branches, and seven on the upper branches. The majority of the larvae released on the upper third of the tree selected the main trunk for cocooning sites with a few choosing the upper and lower branches. Some of the larvae released on the lower third of the tree crawled upwards to spin up on the upper branches, but of those released on the ground the ones that found the tree spun up on the trunk only. The distribution of the larvae on the trunks of the three trees for each one foot section above the ground was:

Level in feet	1	2	3	4	5	6	7
Number of larvae	8	8	8	4	6	5	3

TABLE II

Summary of releases of codling moth larvae in the movement studies.

Test number	Release point or condition	Number of larvae released	Number of larvae locating tree trunk	Number of larvae spinning cocoons in ground	Number of larvae lost
1	A	10	1	8	1
	B	10	0	10	0
	C	10	1	7	2
	D	5	1	2	2
2	E	20	0	17	3*
3	F	30	13	8	9
4	Cloudy weather	22	14	4	4
5	Night	36	26	6	4
	Night	12	4	4	4

*Two larvae did not move and were discarded.

Within each tree the type and amount of the loose scales of bark found at the various levels appeared to have a definite influence on the number of larvae spinning up at each level.

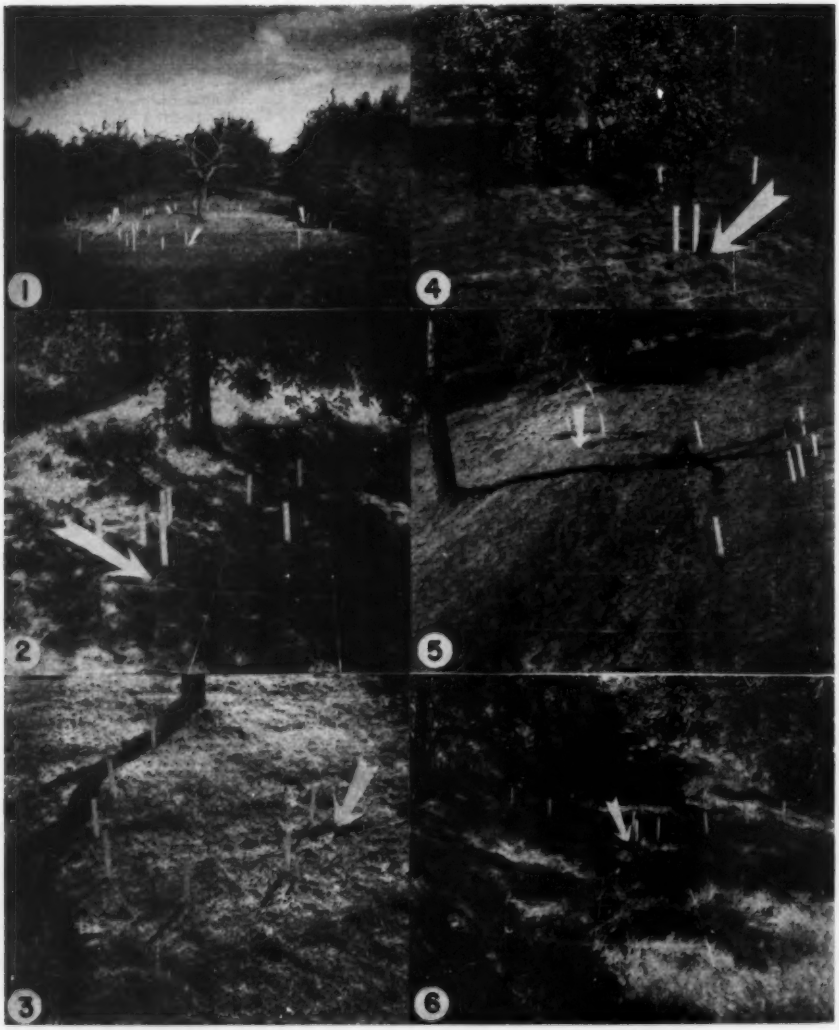
Movement Experiment – 1959

The frequency of the codling moth larvae in finding the tree trunk in the 1958 experiment indicated a distinct preference for this site and implied that factors other than random searching were influencing them in locating cocooning sites. In September, 1959, five tests were designed to investigate the choosing of cocooning sites by codling moth larvae.

In an isolated orchard one apple tree was defoliated by the removal of the smaller branches and the area beneath and surrounding the tree was cleared of the grass undergrowth and excess debris with a power lawn mower and by raking out to the adjacent trees as shown in Figs. 1 and 7. There were no trees in the two rows west of the defoliated tree. The square area enclosed by two adjacent trees in each of two adjacent rows (Figs. 6, 9) and the area beneath a fully foliaged tree (Fig. 10) were also cleared of grass and debris. The clearing facilitated observation and detection of larvae with the particle counter.

In the first test, ten mature larvae were released under sunny conditions at 0900 hr. Atlantic Standard Time at each of three release points which were equidistant from the base of the defoliated tree (Fig. 7). Release point A was in the shadow of the adjacent tree south of the defoliated tree, and release points B and C were in the open, west and north, respectively, of the defoliated tree. One-half hour later five additional mature larvae were released at point D in the open halfway between release point A and the defoliated tree but slightly west of a line connecting the two. Table II summarizes the results of the 1959 experiment.

The larvae released in the shade at point A moved more sluggishly than the larvae released in the sun at points B, C, and D. After a period of orientation that lasted up to 30 minutes or longer, five of the larvae released at point A moved



Figs. 1-6. 1, General view looking east of defoliated tree and area cleared of grass and debris. From left to right arrows show release points C, E, B, and A. White stakes show positions of some of the spin-ups recovered six days after release. 2-5, Release points A, B, C, and E, respectively, showing positions (stakes and small arrows on trees) of spin-ups recovered six days after release. 6, General view looking south of area for the third test showing positions (stakes and small arrows on trees) of some of the spin-ups recovered five days after release. Lighted area under tree number 1 on right was not as extensive as shown in photograph.

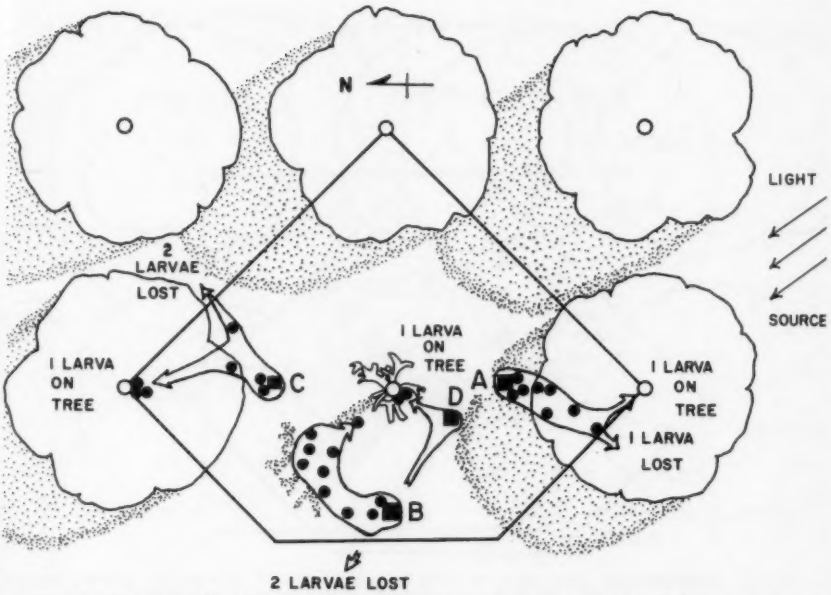


Fig. 7. Diagrammatic plan view of area of first test of movement. Polygon represents cleared area, broad arrows area of movement of mature codling moth larvae, black squares points of release and black dots positions of spin-ups recovered in the ground six days after release.

in a southwesterly direction towards the darkest shadow beneath the nearest tree (Figs. 2, 7). Of the ten larvae released at point A, five spun up in debris on the ground within 50 inches of the point of release, three spun up between 50 and 120 inches, one found the tree trunk and one was lost. The five larvae forming cocoons nearest the point of release did not appear to become fully orientated and roamed about a small area for nearly two hours before finally spinning cocoons. The individual that reached the tree orientated in approximately one minute and moved quickly in a southwesterly direction to the edge of the cleared area, which coincided with the shadow of the tree trunk, orientated again and found the tree trunk. Two others reached the tall grass and attempted to re-orientate but no movement toward the tree trunk occurred: one spun up in debris on the edge of the cleared area and one was lost outside the cleared area where it was difficult to detect radioactivity with the portable survey meter. The two remaining larvae moved about the shadow of the tree for some considerable time before spinning up.

The 25 larvae released at points B, C, and D reacted similarly initially. Seven of the ten larvae at release point B became orientated in less than three minutes and moved quickly in a northerly direction at an angle of approximately 135° with the sun (Figs. 3, 7). On reaching the shadow of the defoliated tree orientation was again attempted and some movement towards the tree occurred. However, none of the seven larvae found the tree trunk. An eighth larva that orientated itself in about two minutes moved in a westerly direction to the edge of the cleared area, reorientated and adjusted to the 135° easterly direction. The two remaining larvae required prodding before they moved. They did not orientate but began to spin up in debris within one-half hour.

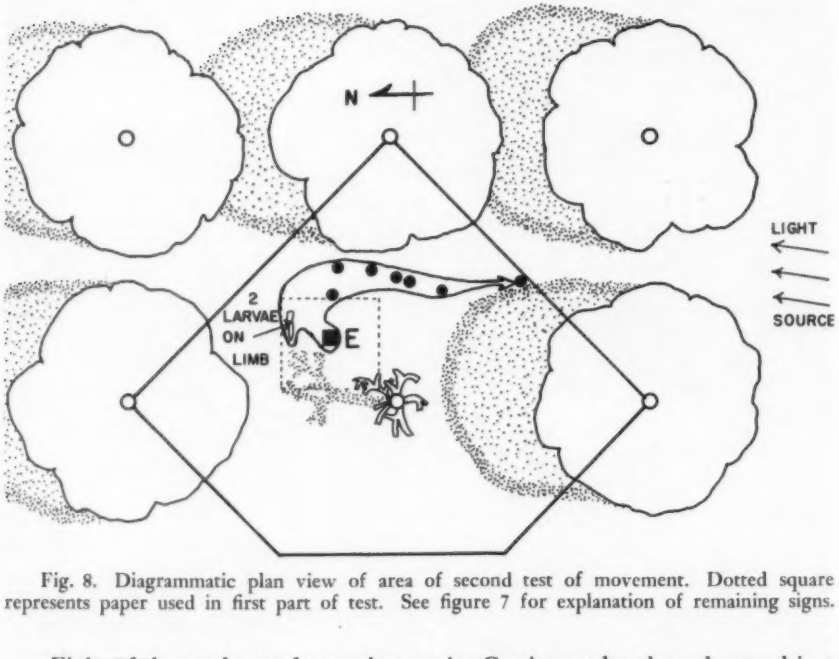


Fig. 8. Diagrammatic plan view of area of second test of movement. Dotted square represents paper used in first part of test. See figure 7 for explanation of remaining signs.

Eight of the ten larvae from release point C orientated early and moved in a northerly direction, also at an angle of approximately 135° with the sun (Figs. 4, 7). Four larvae of this group reached the shadow of the fully foliaged adjacent tree, reorientated and moved towards the tree trunk which one larva ascended. A fifth larva found the shadow but failed to reorientate and a sixth spun up outside the periphery of the tree. Two larvae were lost. The remaining two larvae from point C spun up in debris near the point of release.

The five larvae released at point D were very active and orientated within two minutes. Three of the larvae moved in a northerly direction towards the trunk of the defoliated tree. One larva of this group ascended the tree trunk and two spun up on the ground at the base of the tree. The remaining two larvae moved in a westerly direction and were lost in the tall grass outside the cleared area (Fig. 7).

In the second test ten mature larvae were released in the centre of a large (9 ft. x 9 ft.) sheet of brown wrapping paper at 1300 hr. A.S.T. and at a distance of eight feet northeast of the defoliated tree (Fig. 8). The paper was placed to allow part of the shadow of the defoliated tree to fall across the west edge of the paper. Eight of the larvae began to orientate almost immediately and moved easterly at approximately 135° with the sun. Six of these larvae crawled beneath the paper and spun up in debris, one spun up in debris two feet from the paper and another on a dead apple limb resting on the paper as a weight. The two other larvae remained quiescent at the point of release and prodding would not induce them to move.

The paper was removed and at 1330 hr. a second group of ten larvae were released at the same location on the ground. By this time the shadow of the defoliated tree had moved to within 18 inches of the point of release (Fig. 8).

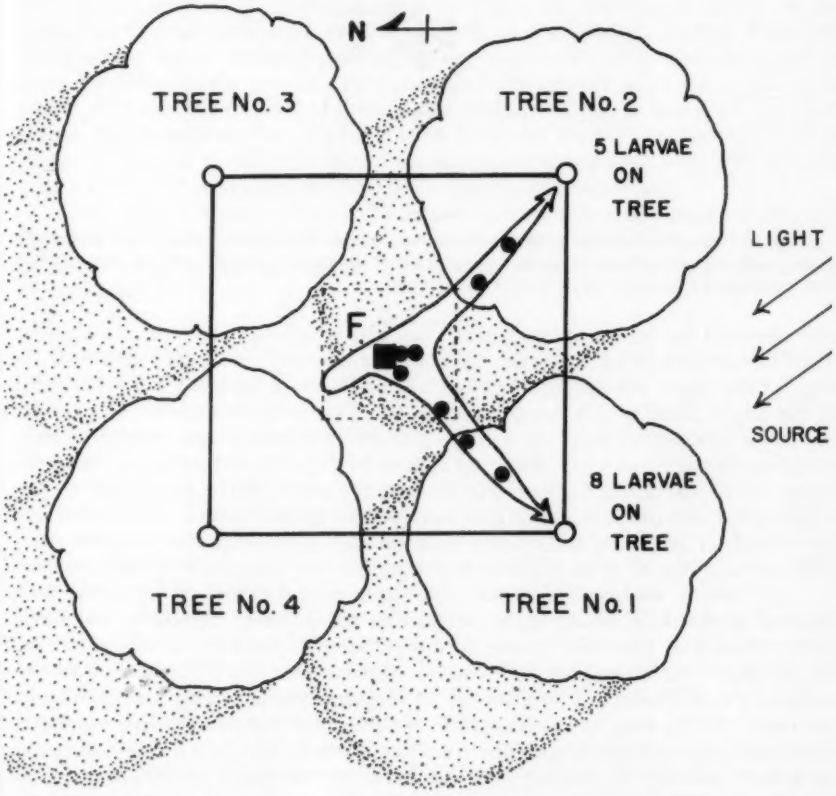


Fig. 9. Diagrammatic plan view of area of third test of movement. Dotted square represents paper used in first part of test. See figure 7 for explanation of remaining signs.

After orientation all ten larvae moved in an easterly direction away from the shadow of the trunk of the defoliated tree. Two spun up on the dead apple limb left on the ground after the removal of the paper. The remaining eight larvae reached the shadows produced by the main branches of the defoliated tree and attempted to reorientate themselves (Figs. 5, 8). None of the larvae approached the trunk of the defoliated tree and seven spun up in debris; one moving to the edge of the cleared area 27 feet distant. The eighth larva of this group was lost.

In the third test ten mature larvae were released in the shade at 0900 hr. A.S.T. in the centre of a nine-by-nine-foot sheet of paper placed equidistant from four adjacent trees as shown in Fig. 9. The ten larvae were generally slow in orientating themselves. One larva moved immediately in a southwesterly direction directly towards tree number 1. It covered the 18 foot distance in 17 minutes and ascended the tree. Some of the remaining larvae required nearly 15 minutes before establishing a direct route. Larvae did not seem to be influenced by the smaller sunlit spots on the paper but light spots with a diameter of six inches or more caused them to stop and reorientate. Under these conditions larvae did not appear to orientate in respect of the sun but merely moved about until a chance direction took them back into shadow. Similar behaviour was

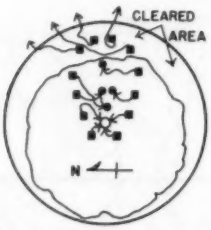


Fig. 10. Diagrammatic plan view showing the paths taken by 12 larvae released at night in an ovoid ring around the trunk of the tree. Black squares represent points of release, black dots positions of spin-ups recovered in the ground.

also observed for larvae released in the sun and which later moved into shadow. Two larvae released on the paper moved northwesterly to a sunlit area near the edge of the paper but reorientated quickly and moved back through the centre of the paper towards tree number 2 (Fig. 9) in the southeast corner of the area. No larvae moved towards tree number 3 in the northeast corner though shadow covered most of this route. As larvae approached the edge of the paper additional strips were put down to give uninterrupted travel. After their routes were established three larvae in this group were picked up and turned about. Following periods of hesitation and reorientation two larvae resumed their original route and the third moved at an angle of approximately 90° from its original direction.

At 1000 hr. the paper was removed and a second group of ten larvae were released in the shade in the same location on the ground. Similarly, ten larvae were released at 1300 hr. These 20 larvae behaved similarly to those released on the paper but movement was slower. A larva that travelled directly to tree number 1 took 45 minutes to cover the 18 foot distance and immediately ascended the tree. Of the total larvae released in the third test eight found tree number 1, five found tree number 2, and nine were lost; three larvae spun up near the point of release and five at varying distances between the point of release and trees numbers 1 and 2 (Figs. 6, 9).

In the fourth test 22 mature larvae were serially released in the southwest quadrant beneath the canopy of tree number 3 (Fig. 9). The releases were made during the morning and the afternoon of a cloudy day at distances chosen at random from four to eight feet from the base of the tree. The larvae required as long a period of time to orientate as did those released in shade and generally moved directly towards the tree but occasionally one would change course, then later move towards the base of the tree again. Movement was not so fast as that of larvae released in the sun but seemed to be equivalent to that of larvae released in shade. There appeared to be a direct relationship between temperature and speed of movement. Of the 22 larvae released 14 found the tree trunk, four spun up in the debris on the ground, and four were lost.

In the fifth test 36 mature larvae were serially released on the ground at night in a circle four feet from the base of a tree in full foliage and an additional 12 released in an ovoid ring about the base. The latter releases were made both beneath and outside the canopy of the tree (Fig. 10).

The larvae released at night could not be observed for orientation movement because it had been decided not to use artificial lights. The portable survey meter was used for the detection of the larvae. The time taken for orientation, however, generally was longer than for any of the other experiments and this may have been due to temperature differences. It was difficult to detect slight changes in direction of travel but major changes were easily followed. Of the

first 36 larvae released, 26 found the tree trunk, six spun up in debris on the ground, and four were lost. Those released on the side of the tree where the canopy was lowest moved towards the tree trunk with little hesitation. However, on the opposite side of the tree where the canopy was higher and from which direction the moon was shining, movement was slower and more irregular. Generally, movement was away from the light and four larvae, moving at right angles to the tree trunk, spun up in the debris on the ground. A fifth spun up near its point of release and a sixth at the base of the tree trunk.

The larvae released in the ovoid ring about the tree trunk behaved similarly (Fig. 10). Those under the darker portions of the tree found the trunk, four others spun up in debris, and the four released outside the canopy were lost in the tall grass.

Discussion

Though the amount and type of debris on the ground in the cocooning experiment appeared to be suitable for cocooning sites only 11 per cent of the larvae recovered used this debris for cocooning. That so many of the larvae released on the ground reached the tree trunk indicated a distinct preference for this site. It also indicated that the trunk was found by other than random searching. Once on the tree, however, searching for cocooning sites did appear to be random. This confirms the observation made by Gnadinger *et al.* (1940). The larvae moved about the tree trunk in all directions and appeared to be completely disorientated. The selection of cocooning sites on the tree trunks depended on the quantity and quality of loose scales of bark. Crevices were commonly used but larvae frequently chose areas of accumulated bark scales. Occasionally a larva would choose an isolated bark scale under which to cocoon. In this experiment there was no visible difference in the amount and type of loose scales on the upper and lower regions of the tree trunks but more larvae chose the lower three feet of the trunks for cocooning sites.

The codling moth larvae used in the movement experiment showed a photonegative response; movement was not directly away from the sun but at an angle of approximately 135° to it. Wellington (1955) has shown that under suitable conditions of the sky, travelling insects consistently turn further away from the sun as the temperature rises; towards it as the temperature falls; and that the plane of polarization of light from the overhead sky at the time travel begins is the factor maintaining the orientation angle, with adjustments in course being caused by temperature changes in the insect and its surroundings. However, when the sun was in view, overheated photonegative *Choristoneura fumiferana* (Clem.) larvae (Wellington *et al.* (1951)) made only a momentary response with a shift of 90° in the plane of polarization. When the sun was fully obscured these larvae reacted more strongly to rotating polarized light. A combination of temperature differences and the plane of polarization of light may have caused the wide variation in direction observed in the movement experiment of individual codling moth larvae released from the same point. Movement away from the release point was at irregular time intervals rather than as a mass movement so that each larva would be subjected to slightly different microclimatic conditions.

Movement of larvae to cocooning sites usually occurs at night (Garlick and Boyce (1940), Garlick (1948)); this may help to explain why the larvae released at night were more successful in finding tree trunks than were those released in daylight. The larvae released under cloudy conditions or at night appeared to move more regularly with little stopping for orientation or change of direction, whereas releases during the day resulted in considerable reorientation depending

upon the amount of shadow and sunny areas present. For some unknown reason some larvae released under the former conditions travelled at right angles to or obliquely towards the tree for some distance before changing to a more direct course.

The speed of movement of the larvae varied with the individual. When larvae were dipped in the radioisotope solution some spun silken threads about themselves. This hindered movement in a few instances. Most larvae moved quickly over the ground, travelling well up on the surface of clumps of grass, small twigs, and other obstacles in the line of travel. Some larvae moved more slowly and appeared to be more cautious, often hesitating at obstacles and usually going beneath them. A few others appeared to explore each obstacle as if seeking cocooning sites. The first larvae to become orientated either initially or later were the fastest moving larvae and were generally more successful in finding the tree trunks than were the slower moving ones. Occasionally an actively moving larva would suddenly stop on the ground for no apparent reason and begin to explore debris or crevices with very sluggish movements. When this happened, cocooning activity usually followed a short time later.

The larvae were watched to see if they followed the fine silken threads left behind by preceding larvae but there was no evidence of this. Six weeks after release 62 (94 per cent) of the larvae spinning up in the ground were eaten by ground fauna. No radioactive predators were recovered.

Summary

The majority of fully-grown codling moth larvae released on fruit on the upper and lower one-third sections of apple trees and on the ground selected the tree trunk for cocooning purposes. Fully grown larvae released in the open moved at an angle of approximately 135° to the sun whereas those released in shade under sunny conditions, during cloudy weather, or at night sought the darkest shadows of various objects. Of the larvae released in the sun four per cent found tree trunks compared with 35 per cent of those released in shade. Of the larvae released under the canopy of the trees in cloudy weather and at night 64 and 68 per cent respectively located tree trunks. Four larvae released at night outside the canopy of an apple tree moved irregularly and none found the tree trunk. These results indicate that codling moth larvae seek the darkest areas for cocooning purposes.

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Nomenclature Notice

In accordance with a decision of the 13th International Congress of Zoology, 1948, public notice is hereby given of the possible use by the International Commission on Zoological Nomenclature of its plenary powers in connection with the following cases, full details of which will be found in *Bulletin of Zoological Nomenclature*, Vol. 17, Parts 6/8, to be published on 8 April, 1960:

(1) Validation of the generic name *Delphax* Fabricius, 1798 (Class Insecta, Order Hemiptera) Z.N. (S)47;
(2) Validation of the family-group name PLEUROCERIDAE Fischer, 1885 (Class Gastropoda). Z.N. (S)83;
(3) Validation of the generic name *Idotea* Fabricius, 1798 (Class Crustacea, Order Isopoda). Z.N. (S)412;
(4) Designation of a type-species for the nominal genus *Macropsis* Lewis, 1834 (Class Insecta, Order Hemiptera). Z.N. (S)456;
(5) Suppression of the generic name *Promecopsis* Duméril, 1806 (Class Insecta, Order Hemiptera). Z.N. (S)483;
(6) Validation of the specific name *dentipes* Guérin, 1832 (*Alpheus*) (Class Crustacea, Order Decapoda). Z.N. (S)643;
(7) Validation of the generic name *Parapenaeus* S. I. Smith, 1885, and interpretation of the nominal species *Peneus membranaceus* Risso, 1816 (Class Crustacea, Order Decapoda). Z.N. (S)645;
(8) Suppression of the specific name *longicorne* Latreille, 1804 (*Acrydium*) (Class Insecta, Order Orthoptera). Z.N. (S)675;
(9) Stabilization of the names of the North European species of the *Tipula oleracea* group (Class Insecta, Order Diptera). Z.N. (S)896;
(10) Suppression of the generic name *Spatagus* Müller, 1776 (Class Echinoidea). Z.N. (S)1195;
(11) Suppression of the generic name *Drepanis* Brisson, 1760 (Class Aves). Z.N. (S)901;
(12) Designation of a type-species for the nominal genus *Sphaerocoryphe* Angelin, 1854 (Class Trilobita). Z.N. (S)1152;
(13) Validation of the familiar usage of the generic name *Tanytarsus* van der Wulp, 1874 (Class Insecta, Order Diptera). Z.N. (S)1245;
(14) Designation of a neotype for the nominal species *Dytiscus cinereus* Linnaeus, 1758 (Class Insecta, Order Coleoptera). Z.N. (S)1389;
(15) Validation of the generic name *Acilius* Leach, 1817 (Class Insecta, Order Coleoptera). Z.N. (S)1391;
(16) Validation of the specific name *dardanus* Brown, 1776 (*Papilio*) (Class Insecta, Order Lepidoptera). Z.N. (S)1403.

Any zoologist who wishes to comment on any of the above cases should do so in writing, and in duplicate, as soon as possible, and in any case before 8 October, 1960. Each comment should bear the reference number of the case in question. Comments received early enough will be published in the *Bulletin of Zoological Nomenclature*. Those received too late for publication will, if received before 8 October, 1960, be brought to the attention of the Commission at the time of commencement of voting.

All communications on the above subject should be addressed as follows:

The Secretary,
International Commission of Zoological Nomenclature,
c/o British Museum (Natural History),
Cromwell Road,
London, S.W. 7.,
England.

W. E. China
Assistant Secretary
International Commission
on Zoological Nomenclature.

March, 1960.

Book Review

A Review of the Crabhole Mosquitoes of the Genus *Deinocerites* (Diptera: Culicidae), by J. N. Belkin and C. L. Hogue, Univ. of Calif. Pubs. in Entom., Vol. 14, No. 6, pp. 411-458, 41 figures. University of California Press, Apr. 22, 1959. Price $1.00.

The species of the genus *Deinocerites* occur from southern Florida and Texas to Brazil; they are of little medical importance but are nonetheless of unusual interest because of their peculiar structural characters and their highly specialized and restricted breeding sites. It was a surprise to find that they had been very poorly known taxonomically until the publication of the paper under review, but this situation has now been admirably remedied as far as available material allowed. The genus is described in detail and its probable relationships are discussed. Detailed descriptions of adults of ten species (compared with four previously recognized) are given; unfortunately larvae of only six and pupae of only three are known, sometimes from imperfect material. The illustrations, by the junior author, are excellent. All available biological data is summarized, and its paucity, and sometimes contradictory nature, are made apparent. The authors speculate at considerable length on the relationships and possible geological history of the various species and species groups; much of this seems premature, especially the suggestion that no less than three species are of probable hybrid origin. When such origin is still a matter of debate in groups for which extensive and varied data is available it seems futile to suggest it in a group whose study has just begun.

J. R. Vockeroth

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